FUNGI AND PLANT DISEASE

BY

B. B. MUNDKUR
M.A., Ph.D., F.N.I.
DIVISION OF PLANT DISEASES, DIRECTORATE OF PLANT PROTECTION AND QUARANTINES, MINISTRY OF AGRICULTURE, NEW DELHI

MACMILLAN & CO LTD

1961

First Edition 1949
Reprinted 1953, 1959, 1961

MACMILLAN AND COMPANY LIMITED
Bombay Calcutta Madras

Printed in Great Britain by Richard Clay and Company, Ltd.,
Bungay Suffolk

TO

M . . . .

WHO FURNISHED THE INSPIRATION FOR UNDERTAKING
THIS ENDEAVOUR,
THIS BOOK IS HUMBLY DEDICATED

B. B. M.

PREFACE

Forty-five years have elapsed since the policy of intensive agricultural development was initiated in India by Lord Curzon, and during that period agricultural education has made considerable strides in this country. At present there are twenty colleges of agriculture, and more are contemplated. In spite of this progress, few books on agricultural subjects for use as text-books by undergraduate students have been published in India. In studying mycology, entomology, agricultural bacteriology, genetics, breeding, farm crops, etc., students have still to rely on books from Europe and America, written primarily for the benefit of the students of those continents, and not very useful to Indian students as text-books.

This book has been written to fill what is considered to be a real need, and I hope that it will be welcomed by teachers and students alike. It is *not* a compendium of *all* the diseases of economic plants occurring in India, but deals with those that are considered important and representative. The subject-matter of the book may in places be somewhat advanced for undergraduate students, but I have done this deliberately, so as to rouse their interest and induce them to specialize in the subject in their post-graduate work. I hope that students of the Colleges of Science and the University Departments of Botany will also find the book useful.

Anyone who undertakes to write a book on Indian plant diseases must be conscious of his indebtedness to Sir Edwin Butler, and a perusal of this book will show how much I owe to him and to his *Fungi and Disease in Plants*. When I wrote to him, before his lamented death, for permission to reproduce some of the figures from his book, he not only gave it but blessed my venture, and to him and to his publishers, Messrs. Thacker, Spink & Co., I wish to express my grateful thanks for granting me this permission. I have also to thank the Department of Agriculture of the Government of India, presided over by Dr. Rajendra Prasad, for permission to use some of the figures from the archives of the Division of Mycology of the Indian Agricultural Research Institute, New Delhi. To my friends Mr. J. F. Dastur and Prof. S. L. Ajrekar, the distinguished

veteran mycologists of India, I desire to express my deep appreciation of the trouble they took in reading parts of the manuscript and making valuable suggestions. Finally I must acknowledge the kindness of numerous friends in India and abroad, and their various publishers, in permitting me to use figures from their publications.

B. B. MUNDKUR

Division of Plant Diseases,
Directorate of Plant Protection and Quarantines,
Ministry of Agriculture, New Delhi.

CONTENTS

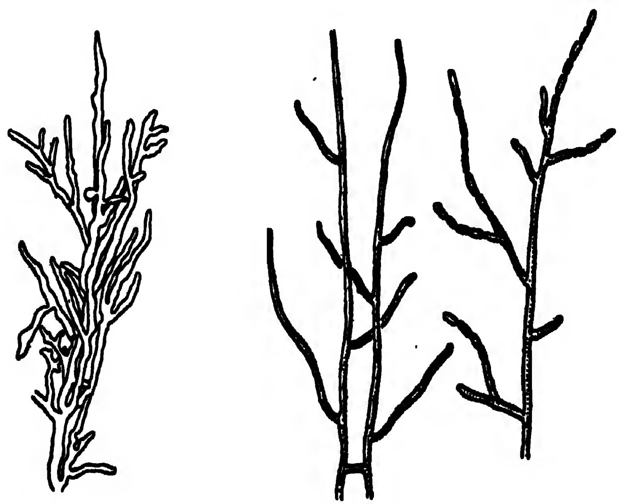
CHAPTER I

FUNGI: THEIR MORPHOLOGY AND REPRODUCTION

FUNGI are thallophytic plants of very varied form and habit, and comprise a large and heterogeneous group. The two chief features that characterize them are: (1) a complete lack of chlorophyll, the green colouring matter which enables higher plants to synthesize carbohydrates from carbon dioxide and water in the presence of sunlight, and (2) reproduction typically by spores. The fungi are delimited from the animal kingdom by the presence of a cell-wall. [The science which deals with their life-histories, relationships and evolutionary processes is known as **mycology**.]

MYCELIUM

The vegetative body of a fungus consists of a network of richly branched filaments known as **hyphae**, and a mass of hyphae is



1 2

FIG. 1.—*1* Coenocytic mycelium; *2* septate mycelium.

termed a **mycelium**. Hyphae grow by terminal and apical elongation. They are segmented into cells by cross-walls which are called **septa**, and the segmented mycelium is known as **septate**. The

septa have a central perforation large enough to permit the streaming of cytoplasm from cell to cell. If a hypha is not segmented it is said to be **coenocytic** (Fig. 1, *1*). In the Phycomycetes there is, as a rule, a total suppression of septation, and the mycelium is therefore coenocytic; septa may be formed during the formation of reproductive bodies, or when the mycelium is damaged, or when there is insufficient nutrition. In the other classes of fungi the mycelium is always septate. In some fungi, like yeasts, the development of the mycelium is limited, and in genera like *Synchytrium* the mycelium is completely absent.

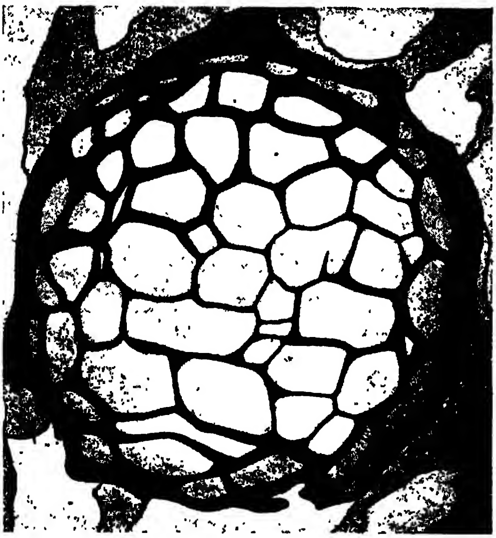


FIG. 2.—Pseudoparenchymatous tissue (sclerotium of *Rhizoctonia bataticola* in section; after Butler).

Hyphae rarely occur singly. Neighbouring hyphae are generally intertwined into felt-like masses, and thick hyphal tissues are formed, as in the fruit-bodies of the higher fungi. These tissues bear a resemblance to the parenchyma of the higher plants, but, as they are the result of the intertwining and union of hyphae, they are termed **pseudoparenchymatous tissues** (Fig. 2).

Hyphae sometimes fuse; in such cases the cell-wall disappears at the point of contact and the two cells open into one another. Two adjacent cells in a hypha sometimes unite by means of a connecting tube, formed around the dividing septum; this tube curves around until its tip reaches the lower cell, with which it fuses; an open passage is thus formed around the septum. Such connections are known as **clamp connections** (Fig. 3). They usually occur at the apical end of the hyphae.

Fungal cells contain cytoplasm, nuclei and vacuoles. They are as a rule uni-nucleate; but a coenocytic mycelium is multi-nucleate. Fungi store their food reserves in the form of oil-drops and glycogen

which is a carbohydrate taking the place of starch of higher plants.

SAPROPHYTISM AND PARASITISM

As fungi lack chlorophyll, they cannot synthesize their essential food requirements. They have therefore to depend on food already synthesized by other organisms. According to the manner in which they obtain their food, they are divided into two classes, **saprophytes** and **parasites**.

Saprophytic fungi live on dead tissues of plants or animals or substances derived from them. They pervade the soil, rotting leaves, plant debris, manure, and in fact every substratum where dead organic matter is found. They play a useful part in continuously breaking down vegetable or animal remains into their constituent elements. Saprophytic fungi are therefore useful scavengers, without the aid of which human or animal life as we know it today would be impossible.

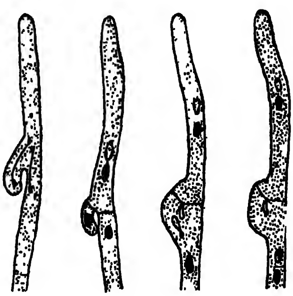


FIG. 3.—Clamp connections; various stages; one on extreme left is that of *Sclerotium rolfsii.*

Parasitic fungi obtain their food from the living tissues of plants or animals which they parasitize, and they are therefore harmful organisms. Some of them attack plants of economic importance, and there is scarcely any crop, whether a garden, orchard, field or forest crop, that does not serve as a host plant for one or more species of fungi.

Among parasites one can distinguish different degrees of parasitism. First, there are those which can never be grown on dead artificial food material. They pass their entire life on living plants only. These are the **obligate parasites,** such as rusts, powdery mildews and downy mildews. Secondly, there are the **facultative saprophytes,** which are usually parasitic in their mode of life, but which can, when the need arises, pass a part of their life as saprophytes. Some of the smuts and leaf-curl fungi belong to this class. On the other hand, there are other species of fungi which usually grow on dead organic matter and are capable of passing their existence saprophytically. Under certain conditions, however, they

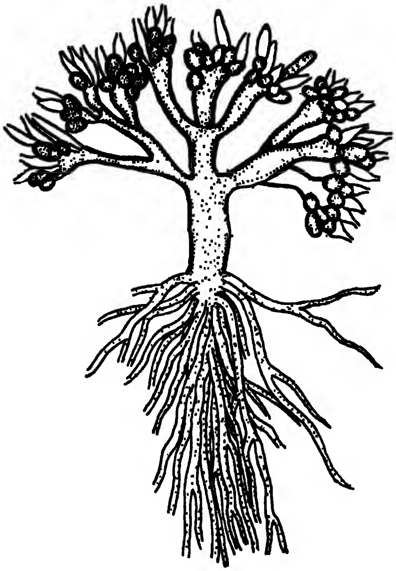


FIG. 4.—Rhizoids of *Blastocladia pringsheimii* (after Minden).

become parasitic. Such fungi are known as **facultative parasites.** Most of the wound parasites which first live on dead tissues caused by the wound and later spread to the living undamaged cells are facultative parasites. Species of the genus *Fusarium*, which cause the wilt disease of numerous plants, are facultative parasites. They live in the soil for considerable periods in a saprophytic manner, but when suitable host plants are sown in such soils they are able to attack them.

One of the functions of the mycelium is that of absorbing nutrition. A part of it may penetrate the substratum as root-like, filamentous and finely branched structures known as **rhizoids** (Fig. 4). If the mycelium lives on the surface of the substratum it is **epiphytic**; but if it is submerged it is **endophytic**.

Parasitic fungi may or may not penetrate the host. If they grow on the surface of the leaves, stems and other parts, the mycelium is known as **ectoparasitic.** Ectoparasites have special outgrowths to serve as holdfasts or organs of attachment, called **appressoria.**

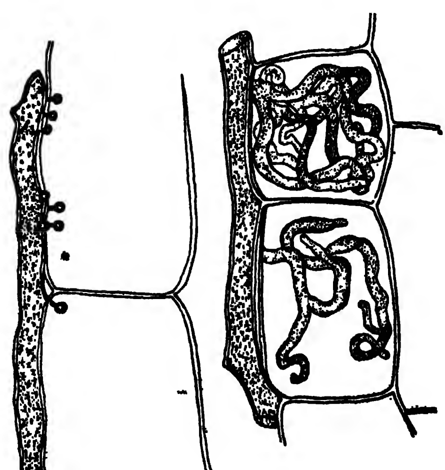


FIG. 5.—Haustoria; on right those of *Peronospora*; on left those of *Cystopus* (after de Bary).

Fungi that penetrate the host and develop their mycelium within the tissues are known as **endoparasites.** This internal mycelium may be restricted to a small area,

as in leaf-spots, or it may be distributed throughout the plant, as in wilt diseases. It may be **intercellular**—that is, lying between the cells—or **intracellular**—that is, lying within the cells. Both ectoparasites and endoparasites possess **haustoria**, which are organs penetrating the cells and which have the function of absorbing food. They may be clavate, lobed, coralloid or filamentous. Sometimes haustoria do not occur, and food is presumably absorbed directly through the unbroken cell-walls. This the fungi are able to do because their cells have a higher osmotic value than those of the host plant.

OVER-WINTERING AND OVER-SUMMERING

Vegetative mycelium is of short duration. After a time it forms **over-wintering** or **over-summering** structures. These struc-

FIG. 6.—Sclerotia of *1 Sclerotium stipitatum* (after Butler); *2* of *Sclerotinia scleriotiorum* on *Eruca sativa* (courtesy P. R. Mehta).

tures can withstand heat, cold and drought, and tide over adverse conditions. The simplest resting mycelium is the **dormant** mycelium of the loose smut of wheat, which is found in the inner tissues of the wheat kernels. Hyphae may intertwine and form pod-like, thick tissues, called **plectenchyma**. A specialized form of such plectenchyma is the **sclerotium** (Fig. 6), which is a more or less rounded or cushion-shaped structure. It consists of a plexus of thick-walled hyphae, the interior cells being hyaline and isodiametric, the exterior dark-brown or black and crust-like (Fig. 2). More

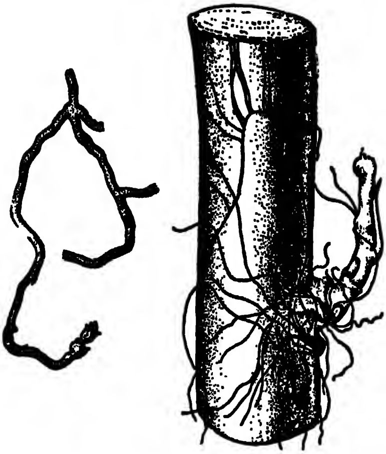


FIG. 7.—Rhizomorphs.

complex are the **rhizomorphs,** in which a number of hyphae grow side by side. They are dark-brown, gelatinous and thick (Fig. 7). They run parallel and adhere to each other, and may be smooth and hair-like, resembling the finer roots of a tree; their diameter, however, is uneven. They can withstand adverse conditions and put forth new growth after a lapse of years.

In addition to these resting bodies, fungi form other kinds of resting cells. In the formation of such resting cells, the hyphae become rounded or angular and envelop themselves with a thick wall. Reserve food accumulates within the cells, and they may even become detached from the hyphae on which they are borne. When conditions are favourable they germinate and put forth a new vegetative body. Such vegetative resting cells, functioning as reproductive bodies, are called **chlamydospores** (Fig. 8). **Oidia** are yet another kind of vegetatively formed cells which arise from the breaking-up of an aerial hypha into a number of equal, rounded segments, functioning also as resting bodies (Fig. 1, *2*). But oidia do not have a resting period, and germinate as soon as suitable conditions are available.

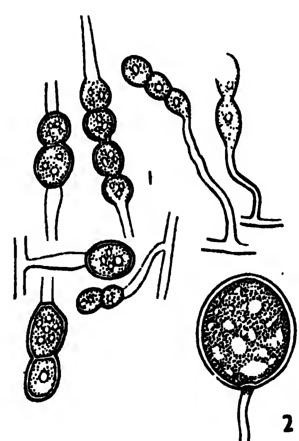


FIG. 8.— Chlamydospores of *1 Fusarium udum*; *2 Phytophthora.*

REPRODUCTION

After growing for a time vegetatively, fungi form reproductive structures. This they accomplish by cutting off specialized cells called **spores.** Spores are the fruiting bodies of fungi, formed in a characteristic manner, with their protoplasmic contents enclosed in a membrane.

The hyphae on which the spores are borne are called **sporophores**, which means spore-bearers. When separated from the mother plant the spores are capable of independent growth into new individuals. They contain one or more nuclei.

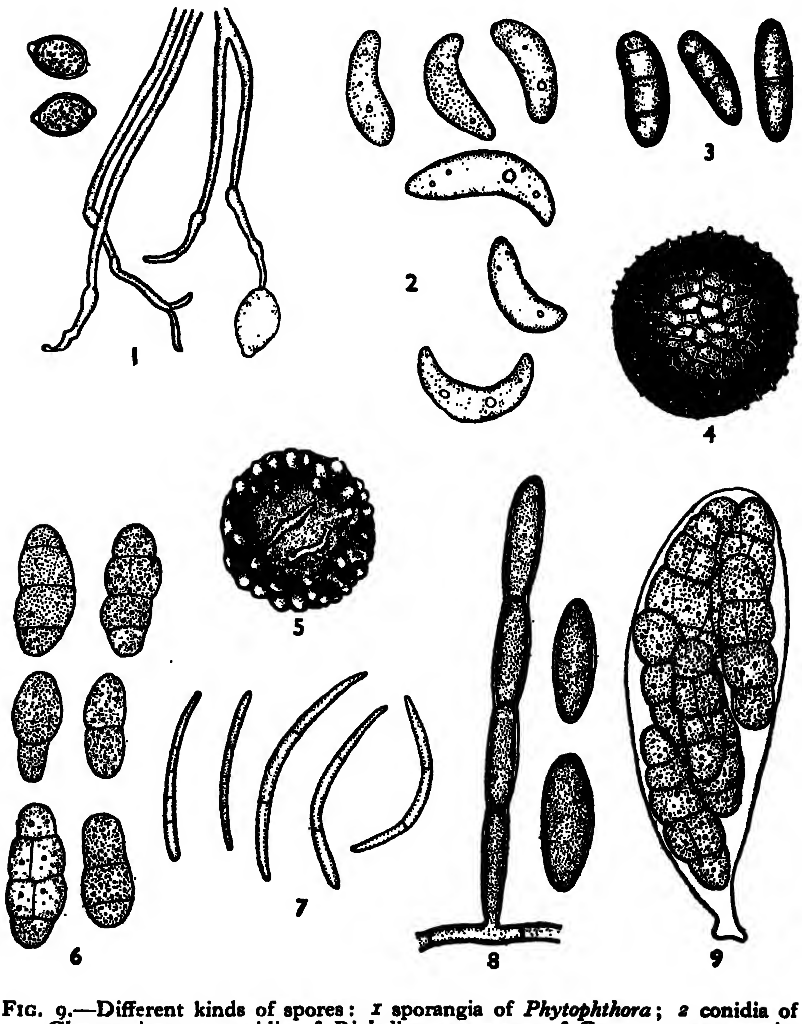


FIG. 9.—Different kinds of spores: *1* sporangia of *Phytophthora*; *2* conidia of *Gloeosporium*; *3* conidia of *Diplodia*; *4* oospore of *Cystopus tragopogonis*; *5* oospore of *Cystopus candidus*; *6* muriform and septate spores; *7* conidia of *Septoria*; *8* conidia and conidophore of *Erysiphe graminis*; *9* ascus with muriform spores of *Pleospora*.

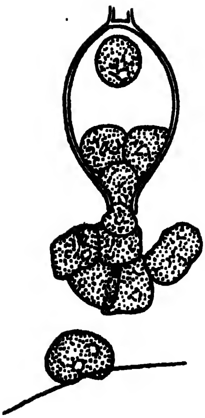


FIG. 10.—Endogenously formed spores, zoospores of *Phytophthora parasitica* (after Dastur).

Spores. Spores are of many kinds (Fig. 9). They differ in shape, size, structure, function and mode of formation. Some of them can resist unfavourable conditions of environment. During the course of its complex life-history the same fungus may produce different kinds of spores at different times, successively or even together. The different spore types of a fungus are, however, alike in the sense that each develops into a plant similar to the mother plant in all its developmental cycles. Fungi with more than one form of spores are termed **polymorphic or pleomorphic.** The Ascomycetes and the Uredinales are particularly rich in polymorphic forms. Polymorphism is confined to the asexual and the haplont stage of a fungus.

Endogenous spores. Spores may be considered from the point of view of morphology, biology and physiology. Morphologically the spores are **endogenously** or **exogenously** formed, **motile** or **non-motile, one-** or **many-celled.** Motile spores are known as **zoospores** or **swarm-spores.** They are endogenously produced (Fig. 10), and the cell within which they are fashioned is known as a **sporangium.** Zoospores are naked, and are provided with one or two flagella whose movements give them a circling or a swarming movement. Sporangia are formed at the end of the sporophores known as **sporangiophores** (Figs. 9, *1* and 12, *1*). Less often sporangia may be formed intercalarily. In the course of evolution the zoospores of some fungi have lost their flagella, and thus their motility. Such endogenously produced, non-motile spores occur in *Mucor*, and are known as **sporangiospores** or **aplanospores,** because even though they are non-motile, they are still formed within the

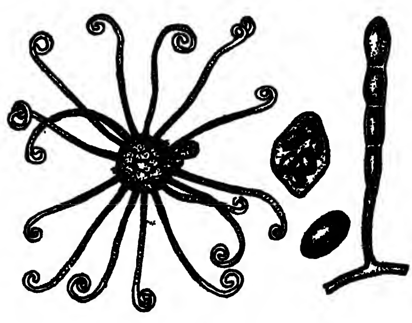


FIG. 11.—Cleistothecia with appendages; also showing asci, ascospores and conidia.

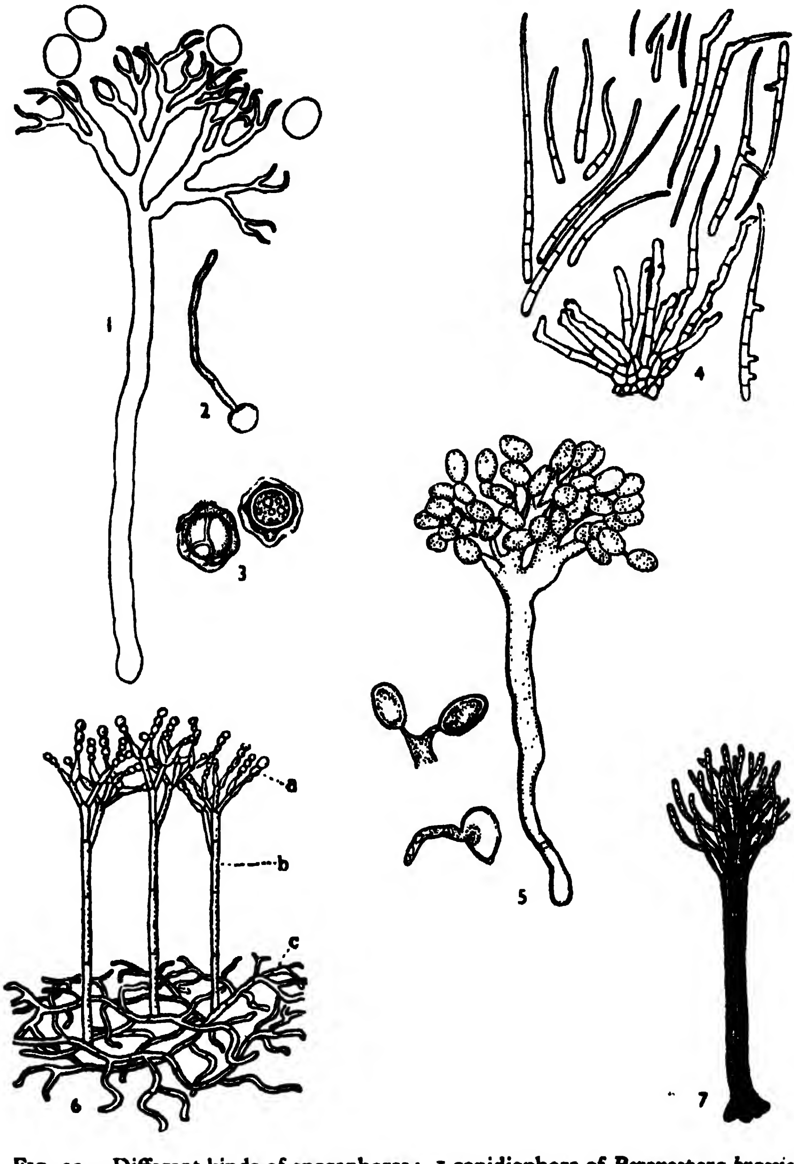


FIG. 12.—Different kinds of sporophores; *1* conidiophore of *Peronospora brassicae* (showing *2* germinating conidium and *3* oospores); *4* conidiophores and conidia of *Cercospora* sp.; *5* conidiophore and conidia of *Sclerospora* sp.; *6* conidiphores of an Imperfect Fungus showing abstriction of conidia and *7* conidiophore of *Arthrobotryum* (*1* and *7* after Butler).

sporangia by cleavage. Zoospores and aplanospores are always unicellular.

Another type of endogenously formed non-motile spore is the **ascospore**, which is formed in an **ascus** (Fig. 9, *9*), which in a majority of cases contains eight such spores. Ascospores may be unicellular or multicellular (Fig. 9, *9*). In the latter case each cell is really a spore capable of germination.

Non-motile spores have a firm cell-wall which is simple or manifold. In the latter case there is a thin hyaline inner membrane —the **endospore**—and a thick, often variously sculptured outer membrane—the **exospore** or the **epispore**. Sculpturing may be in the form of warts, spines, echinulations, reticulations or rings. Various forms of appendages may sometimes be attached to the

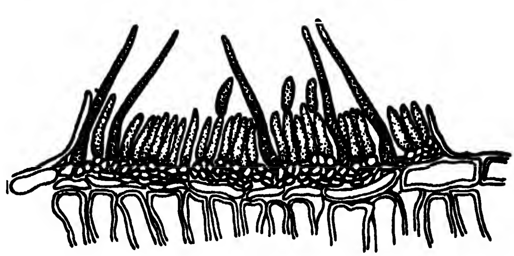


FIG. 13.—Acervulus of *Colletotrichum*, showing setae.

epispore (Fig. 11). Spores vary in colour, but they are as a rule some shade of yellow.

Exogenous spores. Exogenously formed spores are borne on various types of sporophores. The sporophore may consist of a single or branched hypha, or it may be a bundle of hyphae (Fig. 12). It has a vertical position, limited growth and a characteristic mode of branching. The mycelium from which the sporophores arise is often formed into flattened crusts called **stroma**. The stroma is the transitional stage between the vegetative and the reproductive part of the fungus.

When the sporophores form clumps they do so with or without lateral union. When these columns are in fascicles they are called **coremia**. They may also form widespread cushions, to which the name **sporodochia** or **acervuli** has been given (Fig. 13). If they are formed below the surface of the host plant and limited in outline, they are termed **sori** or **pustules**, as in the smuts or rusts (Fig. 14). The spore-bearing hyphae are sometimes enclosed in

roundish, cup- or flask-shaped receptacles known as **pycnia** or **pycnidia** (Fig. 15), and the spores within them are known as **pycniospores, pycnidiospores** or **stylospores.**

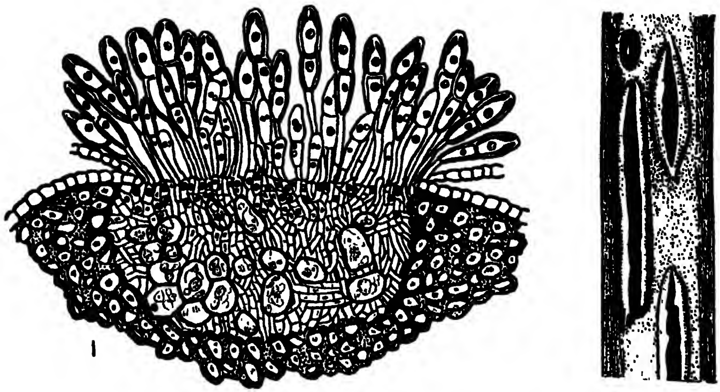


FIG. 14.—Rust sorus and pustule; *1* sorus of *Puccinia graminis*; *2* pustule of *Puccinia glumarum* (after Eriksson).

Sporophores are branched, and such branching is characteristic for the genus and the species. The determination of a genus or the species depends in many cases on the mode of branching of the sporophore.

Spores may not be formed on all parts of the sporophore. In the

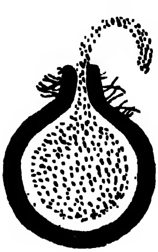


FIG. 15.—Pycnidium and ejection of pycnidiospores.

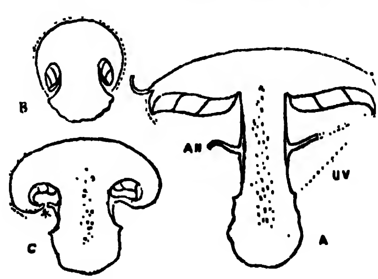


FIG. 16.—Sporophore of *Agaricus campestris.*

mushrooms they are developed on specialized structures—the **gills** —on the underside of the cap (Fig. 16). The part of the sporophore which actually bears the spores is known as the **hymenium.** In a hymenium certain sterile cells or hyphae, usually of a characteristic form, occur intermingled with fertile ones. Such sterile hyphae are

called **paraphyses**, and they are common in the Ascomycetes and the Uredinales.

Asexual spores. Biologically spores may be asexual or sexual. Asexual spores are accessory in character, designed for the rapid propagation and dissemination of the fungus. They are produced in indefinite numbers, always on the haplont mycelium in the Ascomycetes, and, as a rule, on the diplont mycelium in the Basidiomycetes; they are not the result of any sexual act. They may be exogenously or endogenously produced. Exogenous spores are abstricted at the tips of the sporophores, either singly or in chains. Such spores are called **conidia**, and the sporophores bearing them **conidiophores**. Their mode of occurrence, shape, size, colour, septation and markings are of significance from the point of view of taxonomy, even in orders primarily classified by their sexual spores. Asexual spores are the rule in fungi, and in Fungi Imperfecti they form the basis of the system of classification.

Sexual spores. Sexual spores are a result of the union of two or more specialized cells, and indicate a change in the nuclear condition of the thallus. As in other plants, fungi have a phase with a certain fixed number of chromosomes constant for the species, and a phase with double that number. The former is the haploid, and the latter the diploid phase. The former is also known as the **haplophase**, and the latter as the **diplophase**, and the hyphae are called **haplont** or **diplont**, according to the number of chromosomes in their nuclei. When the mycelium changes from the haploid to the diploid phase, a union of two nuclei takes place, though not always immediately, and this is the sexual act in fungi, also known as **conjugation**. The reverse action, when the mycelium changes from the diploid to the haploid phase, leads to a reduction in the number of chromosomes, and the process is known as **meiosis** or **reduction division**.

Fungi may be monoecious, where both sexes occur on the same thallus, or dioecious, where the sexes occur on different thalli. In other words, they may be **unisexual** or **bisexual**. The former are called **homothallic** fungi, and are represented by the ($\pm$) sign, and the latter **heterothallic**, represented by the ($+$) or ($-$) sign, depending on the sexual tendencies shown.

Sex cells arising within a mother-cell are called **gametes**, and the mother-cell a **gametangium**. If the male and female gametes are morphologically undifferentiated, then the process of fertilization is known as **isogamous**. If they differ in size and structure, then

the process is called **heterogamous.** The male gamete is known as an **antherozoid**, and the female as an **egg**.

Sometimes the formation of gametes is suppressed or eliminated and the sex act takes place between two gametangia themselves. This is **gametangial copulation**, and it is the more common form of sex act in fungi. When gametangial copulation is between two morphologically differentiated gametangia, then the male gametangia are known as **antheridia** and the female as **oogonia** or **ascogonia.**

In the lower fungi the conjugation of sex cells or the sex organs is normally followed by a fusion of the haploid nuclei, leading to the formation of a **zygote**, also called a **synkaryon.** The process of fusion of the nuclei is known as **karyogamy.** In the Ascomycetes and other higher fungi, even though the fusion of gametangia takes place, the fusion of the sex nuclei may be delayed, and completed only when the necessity for meiosis arises. The sex nuclei lie side by side in pairs, and are termed **conjugate nuclei** or **dikaryons.** They initiate all vegetative activity synchronously, as though complete karyogamy had taken place. This phase, virtually diploid but containing two sexually differentiated haploid nuclei, is called the **binucleate** or the **dikaryotic** phase.

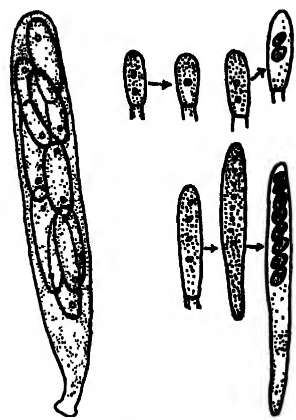


FIG. 17.—Ascus and stages in formation of ascospores by free-cell formation.

The process of fertilization is one of extraordinary complexity. Sexually produced spores are a prominent feature of the Phycomycetes, there being two kinds, **oospores** and **zygospores.** The former are the result of heterogamous, and the latter of isogamous copulation. In the Ascomycetes sexual processes and sex organs are known, but they are not prominent, and in some cases are not completely understood. The sexual spores are formed endogenously within a cell, the **ascus**, by free cell formation, and the spores are called **ascospores** (Fig. 17).

In the Basidiomycetes sexual reproduction is much reduced. There is no real sexual act, but a process of nuclear fusion has been observed which represents sexuality. The sex spores are formed exogenously on a **basidium**, and are called **basidiospores** (Fig. 18).

Spore dispersal. Fungi produce thousands of spores, so that some at least, if not all, may find a suitable substratum and proper conditions for growth. To increase the number of spores, and therefore the chances of survival of the fungus, several devices have developed among the fungi, chief among which are the following:

(1) Production of different kinds of spores by the same fungus: polymorphism.

(2) Increasing the spore-bearing surface: formation of gills.

(3) Increasing the spore-bearing capacity of the same organ: chains of spores, multicellular spores, branching of sporophores.

(4) Producing secondary, tertiary, etc., spores.

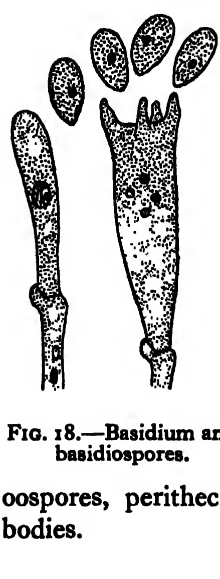


FIG. 18.—Basidium and basidiospores.

Devices for the rapid dissemination of the spores are also common. Spores are liberated by the disintegration of the host tissue, by the hygroscopic movements of the sporophores, by ejection and other means that aid liberation. Their dissemination is effected by wind, water and insects. They may be disseminated through seed, seedlings and nursery stock. Even after successful dissemination fungal spores may not find suitable conditions for growth in the new areas. In such cases fungi form special resting spores or dormant structures known as **hypnospores**, which are able to resist desiccation for long periods without losing their viability. Chlamydospores, oospores, perithecia and teliospores are examples of such resting bodies.

REFERENCES

AINSWORTH, G. C., and BISBY, G. R., *A Dictionary of the Fungi*, 431 pp., 138 figs. Imperial Mycological Institute, Kew. 2nd edition (1945).

BESSEY, E. A., *A Text-book of Mycology*, 495 pp., 139 illus. P. Blackiston's Son & Co., Philadelphia (1935).

BUTLER, E. J., *Fungi and Disease in Plants*, 547 pp., 206 illus. Thacker, Spink & Co., Calcutta (1918).

ENGLER, A., and PRANTL, K., *Die natürlichen Pflanzenfamilien. Fungi.* Band I, Teil 1, Abt. 1 and 1**, Verlag von Wilhelm Englemann, Leipzig (1897–1900); 2nd edition in course of publication.

GALLOWAY, L. D., and BURGESS, R., *Applied Mycology and Bacteriology*, 186 pp. Leonard Hill, Ltd., London (1940).

GÄUMANN, E., and DODGE, C. W., *Comparative Morphology of Fungi*, 701 pp., 406 illus. McGraw-Hill Book Co., New York (1928).
GWYNNE-VAUGHAN, E.; and BARNES, B., *The Structure and Development of the Fungi*, 449 pp., 309 illus. Cambridge Univ. Press, London (1938).
MARTIN, G. W., *Outline of the Fungi*, 64 pp. University of Iowa Press, Iowa City, U.S.A. (1941).
RAMSBOTTOM, J., *Fungi: An Introduction to Mycology*, 80 pp., 23 figs. Ernest Benn, London (1929).
STEVENS, F. L., *The Fungi which Cause Plant Disease*, 547 pp., 449 illus. The Macmillan Co., New York (1913).

CHAPTER II

METABOLIC PROCESSES IN FUNGI

Factors of environment exercise a profound influence on the growth of fungi and on their reproduction, just as they do with other living beings. Not only in rates of growth, but differences in types of growth may occur, depending on such factors. The general term **metabolism** is used for all the processes concerned in the vital activities of plants. Chief among the environmental factors that exercise their influence on metabolism are nutrition, humidity, temperature, light and acidity-alkalinity of the substrate.

NUTRITION

A suitable food supply is essential for the growth and multiplication of fungi. As fungal cells are bounded by cell-walls, they absorb food in solution. Parasitic and other fungi which grow on solid substrates have to convert food into a soluble form before it can be absorbed, and this the fungi do through the action of enzymes which they are able to produce. **Enzymes** are secretion products of fungal and bacterial cells, and are intracellular (**endoenzymes**) or extracellular (**exoenzymes**). Recently they have been isolated in the form of crystalline proteins, their reactions being chemical reactions governed by the ordinary laws of chemistry. They accelerate, and some of them initiate, chemical change, and though they themselves do not enter into the composition of the resulting product, they form a temporary or unstable union with the substances acted upon. One enzyme—**amylase**—can accelerate the hydrolysis of starch and render it assimilable to the fungus. Another enzyme—**cellulase**—can accelerate the liquefaction of cellulose. As already stated, the osmotic value of fungal cells is higher than that of the host cells, so that they are able to absorb food from them easily.

Fungi need hydrogen, oxygen and nitrogen, and smaller amounts of potassium, phosphorus and sulphur. Unlike green plants, which can utilize inorganic carbon as carbon dioxide, fungi are unable to grow unless carbon is provided in an organic form. Traces of other elements, notably magnesium and iron, are also necessary for the

metabolism of fungi. They do not appear to need calcium, which is so essential for the growth of higher plants.

Fungi respire like all other plants, atmospheric oxygen replacing carbon dioxide in the process. Some micro-organisms require free access to oxygen for proper growth, and are termed **aerobic**. Others fail to grow in the presence of free oxygen, and it has to be provided in a combined form. Such organisms are known as **anaerobic.** Germination of spores of several fungi is dependent on the presence of free oxygen. If free oxygen is not present in abundance, spores of several fungi fail to germinate.

HUMIDITY

Little work has been done on the water requirements and transpiration of fungi. Some spores, especially the resting spores, have been supplied with mechanisms for resisting desiccation over long periods. But for their germination, as indeed for that of all fungi, relatively high humidity is necessary. Many fungi grow well if immersed in water, and some are normally found submerged in it. These are the **aquatic fungi** and belong, as a rule, to the Phycomycetes. Some fungi that grow in liquid media form, however, a thick hyphal mat on the surface, and the reproductive structures are produced on the aerial mycelium alone. A majority of the species grow well and reproduce only on solid substrates, but they need high humidity, as their growth is slower at lower humidities. Spores of many fungi fail to germinate if they are immersed in water, primarily owing to want of oxygen. If they are floated on the surface they germinate in large numbers. In a majority of cases the best germination takes place when humidity is over 90 per cent.

TEMPERATURE

Fungi react to temperature in much the same manner as green plants. There is a minimum below which a fungus ceases to grow, an optimum where the best growth takes place, and also a maximum above which it cannot grow. These are the limiting temperatures which admit of growth as distinct from loss of viability. Even though fungi cannot grow above the maximum or below the minimum, they can withstand exposure to higher or lower temperatures without their viability being impaired. Indeed, the spores of some fungi have to be frozen as a preliminary treatment before they can be made to germinate. The teliospores of *Melampsora lini*, the

linseed rust, germinate only when they are subjected to freezing temperature for long periods. Somewhere above the maximum temperature for the growth of the fungus is a temperature exposure to which kills it in a relatively short period of time. This is the **thermal death-point** of the fungus. The thermal death-point may be very high; in *Byssochlamys fulvus* it is as high as 90° C.

The optimum temperature for the growth of the mycelium of a fungus need not necessarily coincide with that for the abundant spore production or for the best germination of the spores. The optima for these latter processes may be, and usually are, different from those for the best growth of the mycelium. Even the pathogenic activity of a fungus may be influenced by temperature. In sann-hemp wilt the temperature for the optimum growth of the causal organism, *Fusarium udum* var. *crotalariae*, is 25–28° C., and coincides with that for the maximum development of the disease. Above 28° and below 25° C. the intensity of the disease diminishes. In the case of blights of wheat and maize, however, the facts are otherwise. The same fungus—*Gibberella zeae*—is responsible for these blights, but the best temperatures for their production are different. A severe blight of wheat is caused at a relatively high temperature—20–28° C.—and of maize at a relatively low temperature—16–20° C. Here the deciding factor is determined by the host. In wheat, for example, certain organic substances which are necessary for the nutrition of the fungus are produced only at a high temperature. In maize the same substances are produced at a low temperature. The ability of the pathogen to attack these hosts is determined, therefore, by the presence or absence of these substances. Furthermore, wheat grows best at relatively low temperatures, and when it is grown at higher temperatures its metabolism is altered, rendering it susceptible to fungal attack. Maize, on the other hand, grows best at relatively higher temperatures, and when it is grown at slightly lower temperatures, it suffers similarly.

Temperature can exercise considerable influence on the production of reproductive bodies. Many of the parasitic fungi occur in the summer months in the imperfect state, producing the summer spores. They form the perfect states later in the season, when temperatures are cooler. *Venturia inaequalis*, the fungus that causes apple scab, produces the conidia (*Fusicladium* stage) in summer. Later, when cooler conditions prevail, the perfect or *Venturia* state is produced. The perfect state of *Sclerotium rolfsii*,

which is known as *Corticium rolfsii*, occurs only when the dishes in which the fungus is growing are exposed to a higher temperature of 35–40° C.

LIGHT

No generalizations are possible concerning the influence of light on the growth of fungi. Some grow well in light, and others in darkness. For the best growth of edible mushrooms dark caves with diffuse light are preferred. Sclerotia of *Sclerotinia sclerotiorum* placed in moist sawdust at a low temperature in a dark room form only the apothecial-initials. They develop into apothecia as soon as they are exposed to bright light.

Light exercises a good deal of influence on the germination of spores of certain fungi. Ultra-violet light, direct sunlight and strong but diffuse light inhibit the germination of the teliospores of *Puccinia graminis*. If the dishes containing the spores placed for germination are covered by green light filters, then normal germination takes place. The pigments occurring in the walls of spores may thus have a protective rôle against injury from strong light. On the other hand, ultra-violet radiation has been shown to exercise considerable influence on the development of the fruit-bodies of some fungi. Stevens obtained the perfect state of *Colletotrichum lagenarium*, which causes an anthracnose of cucurbits, by exposing vigorously growing cultures in petri dishes to ultra-violet rays. The stimulus acting in these cases may be on the protoplasm, or it may be on the nuclei, and is probably due to the production or destruction of some intra-cellular substances affecting cell-activity. It may also be an expression of the law that a well-nourished mycelium, suddenly inhibited in growth, turns to reproduction. Prolonged exposure to ultra-violet rays is, however, harmful to fungi, for they have fungicidal properties.

REACTION TO STIMULI

The effect of acidity and alkalinity (hydrogen–hydroxyl-ion concentration) on the growth of fungi has been investigated. Fungi tolerate wide variations of hydrogen and hydroxyl-ion concentrations, provided other conditions are normal. A slightly acid medium seems to be favourable for the good growth of several fungi. One fungus—*Sclerotinia americana*—shows remarkable tolerance to acidity. Good growth takes place between 1·4 and 5·8 *p*H, and the optimum is near 2·5 *p*H. Apothecia develop in soils only with an

acid reaction. Their development is inhibited if the *p*H of the soils is 6·8 or more.

Fungi respond to physical and chemical stimuli. They grow in response to moisture (**hydrotropism**), oxygen (**aerotropism**) or chemicals (**chemotropism**). Such response may be positive or negative, and different at different periods of growth. Broadly speaking, there are three periods of growth in the life of a fungus. They are: (1) the vegetative phase, (2) the phase of asexual reproduction and (3) the phase when sex organs are formed. These phases are interrelated, but conditions optimum for one phase are not the same for another. In 1900 Klebs proposed the following generalizations regarding the response of lower organisms to environmental conditions:

(1) Growth and reproduction depend on different conditions; among the lower organisms probably external conditions determine whether vegetative growth or reproduction takes place.

(2) Conditions that favour vegetative growth do not favour the production of reproductive bodies. For the latter the conditions should be such as are unfavourable for vegetative growth.

These conditions appear to hold good, barring genetic disturbances. They apply to obligate parasites as well, but attention in their case has to be concentrated on the host, for that is the substratum on which they grow.

REFERENCES

DICKSON, J. G., "Influence of soil temperature and moisture on the development of seedling blight of wheat and corn caused by *Gibberella saubinettii*," *Jour. Agric. Res.*, **23**, 837–870 (1923).

DILLON WESTON, W. A. R., "Effect of light on urediniospores of black stem rust of wheat, *Puccinia graminis tritici*," *Nature*, **128**, 67–8 (1931).

EZEKIEL, W. N., "Hydrogen-ion concentration and the development of *Sclerotinia* apothecia," *Science*, n.s., **59**, 166 (1923).

KAUFFMANN, C. H., "Kleb's theory of the control of developmental processes in organisms and its application to fungi," *Proc. Internat. Congr. Pl. Sci.*, **2**, 1603–1611 (1929).

MUNDKUR, B. B., "A *Sclerotinia* rot of *Hibiscus sabdariffa* L.," *Indian J. Agric. Sci.*, **4**, 757–778 (1934).

MUNDKUR, B. B., "The perfect stage of *Sclerotium rolfsii* Sacc.," *Indian J. Agric. Sci.*, **4**, 779–781 (1934).

STEVENS, F. L., "Effects of ultra-violet radiation on various fungi," *Bot. Gaz.*, **68**, 210–215 (1928).

UPPAL, B. N., and KULKARNI, N. T., "Studies in *Fusarium* wilt of sann-hemp: (I) The physiology and biology of *Fusarium vasinfectum* Atk.," *Indian J. Agric. Sci.*, **7**, 413–442 (1937).

CHAPTER III

DISEASES CAUSED BY FUNGI

Fungi cause disease in plants, animals and human beings. They are sometimes responsible for much damage and destruction. A diseased plant can be easily distinguished from a healthy plant; but it is not possible to frame a precise definition of disease which will meet all requirements. Diseases may be caused by factors of environment or by living entities. The latter may be of either plant or animal origin. A majority of diseases are caused by the invasion of a definite organism. Sometimes the presence of an organism within the tissues of a plant does not denote disease. Roots of leguminous crops are attacked by a bacterium, resulting in the formation of nodules or galls. Far from being injurious, the presence of this bacterium is essential for the normal development of the plant. In parts of the Punjab and Sind the growing of berseem (*Trifolium alexandrianum*) has become impossible because of the absence of the proper bacterium in the soil to infect the roots.

SYMBIOSIS

The living together of two organisms for their mutual benefit is known as a **symbiotic relationship.** The bacterium mentioned above is capable of fixing nitrogen from the atmosphere, and the energy required for its growth is furnished by the carbohydrate of the host. The nitrogen compounds required for the growth of the host are provided by the bacterium. It will be noted that both derive mutual benefit. In some cases, however, one partner may begin to live increasingly at the expense of the other, and a gradual transition from a healthy condition to one of disease takes place; the relationship then becomes one of parasitism.

DISEASE IN PLANTS

A plant develops and functions in a normal manner over a certain range of conditions. If, however, it diverges from the normal and the abnormalities are sufficiently extensive to impair its very existence temporarily or permanently, then it may be considered as diseased.

A disease, then, is a condition of the plant brought about by the inroads made by a causal organism or an unfavourable environment. It is a resultant of all the processes initiated by the disease-producing entity. The study of disease of plants due to an organism or an unfavourable environment is covered by the science of **plant pathology**.

In a plant disease caused by a fungus, the latter may be restricted to a particular area or it may be spread over a considerable area. In the majority of the leaf-spot diseases the fungus is restricted to the precise area of the spot, but in a disease like wilt the parasite occurs throughout a major portion of the vascular tissues. For example, *Cercospora nicotianae*, which causes the 'frog-eye' spot disease of tobacco leaves, does not occur outside the area outlined by the spot; in cotton wilt, on the contrary, the parasite, *Fusarium vasinfectum*, can be detected in the vascular tissues in the roots, stems, branches, and in advanced cases in the petioles of the leaves. *Ustilago kolleri*, which causes the covered smut of oats, attacks the host in the seedling stage and keeps on growing with the host without causing any apparent injury. At the time of ear formation, however, the fungus manifests itself when the ovaries are replaced by the sori which contain the spores of the fungus. Such diseases are known as **systemic** diseases.

A pathogenic fungus, when it attacks its host, more or less rapidly kills the tissues. This killing is known as **necrosis**. The diseased part of the plant where such necrosis has taken place is known as a **lesion**.

SYMPTOMS

The symptoms of disease due to a fungus are very important. They yield clues that lead to the discovery of the nature of the disease, and indicate where the causal organism should be looked for and how it can be controlled. A fungus may kill a plant in the pre-emergence stage or the seedling stage. Others may affect the roots, stems, leaves, inflorescence, flowers or fruits. Sometimes the same fungus may be responsible both for the seedling phase of the disease and the disease in the adult plant. *Helminthosporium oryzae*, for example, causes a seedling blight of rice plants, and, later, adult plants are also attacked, causing spots on the leaves and sterility in the ears.

Rotting. Seeds sown in moist soil may be rotted by the action

of pathogenic fungi. In such cases the pathogens may have been present in or on the seed or the soil, excessive moisture promoting

FIG. 19.—Damping of chilli seedlings: 1 untreated plants; 2 treated with formaldehyde dust.

their pathogenic activity. Poor stands of peas and of gram have recently been investigated, and it has been discovered that the seeds had been rotted in the pre-emergence stage by the more virulent strains of *Fusaria*, which ordinarily would have produced wilt in the adult plants. Such rotting, it may be mentioned, is distinct from the rotting of non-viable seed due to mould action.

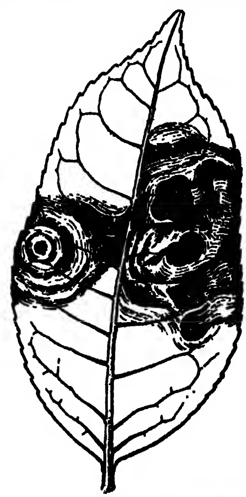


FIG. 20.—Tea leaves affected by brown blight (*Glomerella cingulata*) causing leaf-spots with target-spot-like effect (after Butler).

Damping-off. Various soil-inhabiting fungi, usually saprophytic in their mode of life, cause **damping-off** of seedlings under certain conditions. Species of *Pythium* and *Rhizoctonia* are the most important among such fungi. They attack the foot of the stem or the crown of the roots, rendering the tissues at that region weak, with the result that the seedlings collapse. In chilli, tobacco and tomato seed-beds, large numbers of seedlings succumb to damping-off, and the mortality is often very high (Fig. 19).

Leaf-spots. Leaf-spots are the more important and familiar among the symptoms produced by fungi. Brown being the characteristic colour of dead tissue, it is also the colour of many leaf-spots. They may be minute or several millimetres in diameter. In a spot there may be concentric bands of different shades of brown,

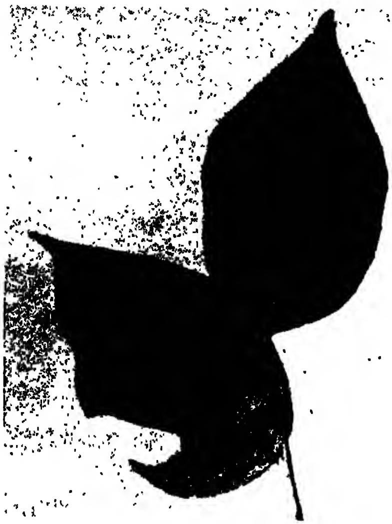


FIG. 21.—Tar-spots.

as in the blight of tea due to *Glomerella cingulata* (Fig. 20). Concentric rings of brown and black are characteristic of several leaf-spots due to species of Melanconiales and Moniliales. Fungi belonging to Phacidiales (*Rhytisma*) or Dothideales (*Phyllachora*) cause black spots which are slightly raised. Such spots are known as **tar-spots** (Fig. 21). Spots due to rusts are brownish or orange-red at first, as that is the colour of the urediospores. Later, when the darker teliospores are formed, the colour of the spots changes to brownish-black. Spots caused by *Cystopus candidus*, the white rust of cabbage, are white, as the name indicates (Fig. 22, *1*). In some leaf-spots the dead tissue of the spot is sometimes shed, leaving a circular perforation called a **shot-hole** (Fig. 22, *2*).

FIG. 22.—*1* Spots due to white rust on mustard leaves; *2* shot-hole.

Discoloration of the leaves may be diffuse or general. In plants suffering from wilt or root-rot the leaves look paler, or even slightly etiolated or bleached. In maize plants attacked by *Sclerospora philippinensis* the leaves turn whitish and chlorotic, owing to the disappearance of chlorophyll, in long streaks. Ectoparasites like powdery mildews give the leaves a greyish appearance, due to the

spores of the fungus. Sometimes the leaves turn yellow and etiolated, as in citrus seedlings attacked by *Oidium tingitanium*.

FIG. 23.—Streaks due to flag smut, *Urocystis tritici*.

FIG. 24.—Stripes due to yellow rust, *Puccinia glumarum*.

Some fungi cause streaks or stripes on the leaf-blades. *Urocystis tritici* causes blackish-brown streaks on wheat leaves (Fig. 23). The yellow rust of wheat due to *Puccinia glumarum* causes regular stripes

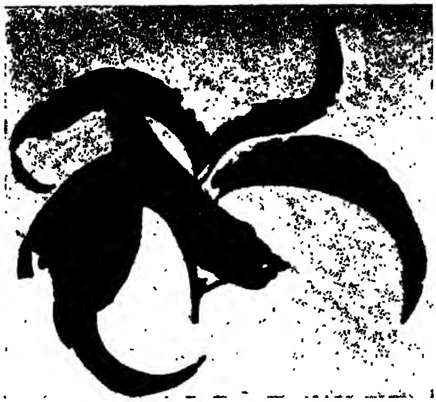


FIG. 25.—Leaf-curl of peaches.

FIG. 26.—Cankers: *1* apple stems affected by *Coniothecium chomatosporum* (courtesy A. Ginai); *2* cankered twigs of almond.

on the leaf-blades, and the rust is therefore known as 'stripe rust' in the United States of America (Fig. 24).

Leaves may become puckered, crinkled or curled as a result of fungal attack. Peach leaf-curl due to *Taphrina deformans* is a good example of leaf-curl (Fig. 25). Galls may sometimes be formed on the surface of the leaves. Minute galls caused by *Synchytrium*

FIG. 27.—Canker due to *Sphaeropsis malorum* on apples, showing pycnidia.

collapsum are common on the leaves of *Clerodendron infortunatum* in several parts of India.

Cankers. Parasitic fungi attack the bark of plants, causing the death of tissues. When the bark sloughs off, open wounds are formed which are often of a spreading nature. They may sometimes be surrounded by a raised, tumour-like margin (Figs. 26 and 27), and are known as **cankers.** Cankers may encircle the entire plant, killing

the upper part of the host. This happens in the pink disease of rubber caused by *Pellicularia salmonicolor*, or in apple-trees attacked

FIG. 28.—Large canker due to stem-bleeding disease of areca-nut tree (courtesy K. M. Thomas).

by *Physalospora mutila* (Fig. 27). In some diseases, such as the stem-bleeding disease of coco-nuts, there is no canker formation, but the bark may crack and a liquid ooze out (Fig. 28).

Foot-rot and Root-rot. In foot-rot of plants the stem at the

level of the soil rots, though the parts above and below are more or less intact. When the foot-rot finally girdles the entire plant the translocation of sap is interfered with, and the plant ultimately succumbs to the disease. In root-rots, on the contrary, the tap root and the secondary root may rot owing to fungal attack, the result being the death of the plants. Death in such cases is sudden, the entire crown showing symptoms of sudden wilting. In black shank

FIG. 29.—Black shank of tobacco due to *Phytophthora nicotianae*.

of tobacco plants the causal organism, *Phytophthora nicotianae*, attacks the foot of the host and brings about sudden death (Fig. 29), whereas in root-rot, such as that of cotton, the causal organism, *Rhizoctonia solani*, attacks the root-system, which it completely destroys. In the Madras and Bombay provinces the rhizomes of ginger are completely rotted by *Pythium myriotylum* and *Pythium aphanidermatum*.

Wilts. Wilts are primarily diseases of the roots, as the causal organisms attack them in the seedling stage. The diseases, however, manifest themselves in the above-ground parts. The onset of the

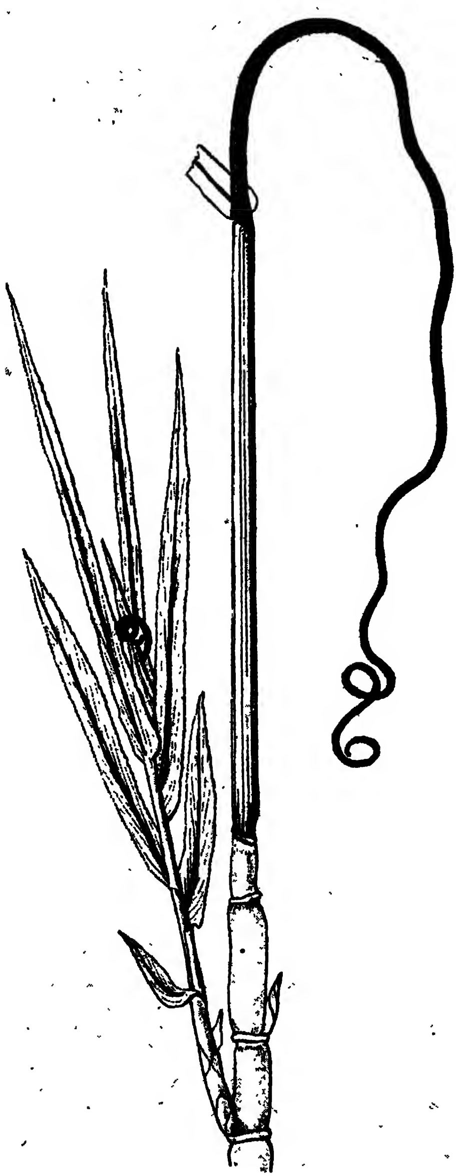


FIG. 30.—Smut whip of sugar-cane.

symptoms in the host is gradual. First the succulent shoots and leaves become limp during bright periods of sunshine. The leaves may show the symptoms of mottling, as in cotton wilt. The flaccid parts gradually wither, droop and finally succumb to the disease. The fungus, after invading the plants, confines itself to the vascular tissues. It is suggested that the fungus secretes a toxic substance that kills the living tissues concerned in the ascent of sap to the growing region. The result is that the plant withers, wilts and dies. The fungus may also clog the xylem vessels and interfere with the free flow of sap.

Disease symptoms in the inflorescence. The symptoms in the inflorescence may be complete destruction, suppression, alteration of the floral axis or of the flowers. The extreme case is the sugar-cane smut, where the floral axis is transformed into a black, dusty whip by *Ustilago scitaminae* (Fig. 30). In the loose smut of wheat the axis is not affected, but the fungus,

Ustilago tritici, destroys the flowers (Fig. 89). In the grain smut and long smut of jowar, the causal organisms, *Sphacelotheca sorghi* and *Tolyposporium ehrenbergii* respectively, destroy the ovaries, which are replaced by the smut sori (Figs. 93 and 87). Large sclerotia take the place of ovaries in rye affected by *Claviceps purpurea* (Fig. 31), and in bajra attacked by *Sclerospora graminicola* the solid spicate ear is wholly or partly turned into a loose green head composed of a mass of twisted leaves (Fig. 58). When sarson (mustard) plants are attacked by *Cystopus candidus*, the petals are turned into sepals and the stamens into carpels (Fig. 32). Rotting of flowers, as in *Hibiscus rosa-sinensis* attacked by *Choanephora infundibulifera*, shedding of flowers, as in the mango inflorescence attacked by the mildew, *Oidium mangiferae*, or exudation of sugary substances, as in the sugary disease of jowar caused by *Sphacelia sorghi*, are some of the other symptoms manifested in the inflorescence.

FIG. 31.—Sclerotia of *Claviceps purpurea*.

Hypertrophy and atrophy. Dwarfing and stunting of entire plants or some particular organs of the plant are due to fungal invasion. Mustard plants attacked by the root-gall-forming smut, *Urocystis brassicae* (Fig. 33) are dwarfed as a result of the attack by the fungus. Abnormal enlargements of varied character are found in plants attacked by fungi, resulting in the formation of tumours, knots, galls or warts. Increase in size due to the enlargement of the component cells or to increased cell division is known as **hypertrophy**. If hypertrophy is due to increased cell division forming a large number of component cells, then it is called **hyperplasia**. Sometimes parts of plants may be arrested in their growth, and they may even be entirely suppressed. This is known as **atrophy**. In sarson plants attacked by *Cystopus candidus* the flower-stalks and other floral parts become swollen owing to hypertrophy, the pistil especially being hypertrophied into an enormously swollen conical sac. When the same plant is attacked by *Peronospora brassicae* there is a suppression of floral buds. This is due to atrophy.

Witches' brooms. Woody plants sometimes produce closely

FIG. 32.—Distortion of mustard inflorescence due to attack by *Cystopus candidus*.

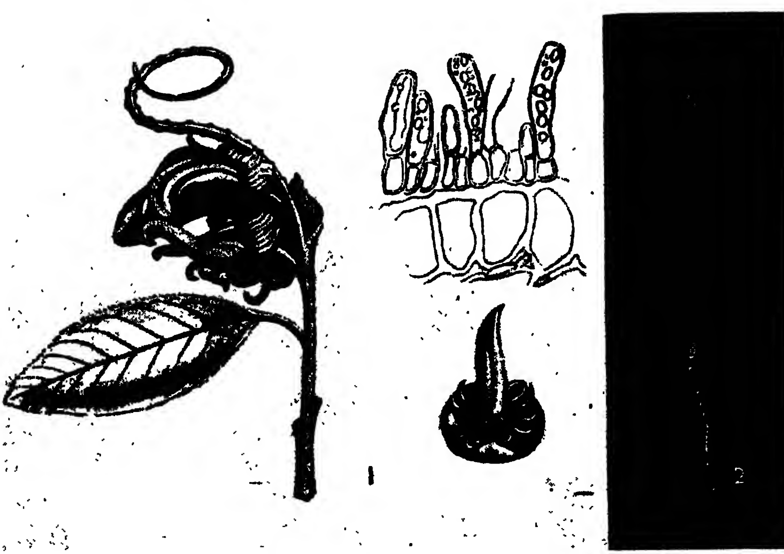


FIG. 33.—*1* Distortion of inflorescence of *Prunus padus* attacked by *Taphrina pruni* (also showing asci); *2* gall-formation of mustard roots attacked by *Urocystis brassicae*.

FIG. 34.—*1* Aecial galls due to *Uromyces hobsoni* on *Jasminum* sp. (courtesy M. J. Thirumalachar); *2* galls on maize plants due to attack by *Ustilago maydis* (courtesy A. Ginai).

FIG. 35.—Witches' brooms of mango inflorescence and of bamboo.

grouped clusters through the formation of irregular tufts by the slender branches. The branches from which such tufts develop may become swollen. They are turned upwards and bear small hypertrophied leaves. These disfigurations are in many cases produced by parasitic fungi whose mycelium infests the internal tissues of the plant. These structures are **witches' brooms.** The witches' brooms of deodar are caused by *Peridermium cedri.* Both hypertrophy and atrophy may be responsible for such development (Fig. 35).

FIG. 36.—Gummosis of cherry.

Gummosis and exudations. The production of a clear, amber-coloured exudate on the surface of the affected parts of a plant, which later sets into a solid mass insoluble in water, is termed **gummosis** (Fig. 36). Gummosis is common in cherry, peach and citrus trees. A reddish exudate is a common feature of the stem-bleeding disease of coco-nuts due to *Ceratostomella paradoxa.*

Other symptoms. Fungi can cause an alteration in the habit, the symmetry or in the maturing of plants. The common weed *Launea asplenifolia,* which usually has an unbranched stem and rosette-like radical leaves, develops into an elongated, many-branched axis with cauline leaves as a result of attack by *Puccinia butleri.* The leaves of jowar become shredded and twisted when attacked by *Sclerospora sorghi* (Fig. 63, *1*). Wheat plants attacked by *Ustilago tritici* come into ear four to five days before the healthy plants.

REFERENCES

BUTLER, E. J., *Fungi and Disease in Plants*, 547 pp., 206 illus. Thacker Spink & Co., Calcutta (1918).

HEALD, F. D., *Manual of Plant Diseases*, 953 pp., 259 illus. McGraw-Hill Book Co., New York (1933).

MELHUS, I. E., and KENT, G. C., *Elements of Plant Pathology*, 493 pp., 259 illus. The Macmillan Co., New York (1939).

OWENS, C. E., *Principles of Plant Pathology*, 629 pp., 222 illus. John Wiley & Sons, New York (1928).

CHAPTER IV

METHODS OF STUDYING PLANT DISEASES

METHODS of studying plant diseases are as varied as the diseases themselves, and only a few general observations can be made. Careful observation of the precise symptoms which a pathogenic fungus causes in the host plant is of primary importance. The correct identification of the parasite and the definite establishment of its parasitism then demand attention. In smuts, rusts and powdery mildews the parasite can be located in the lesions on the host, and their parasitism can be taken for granted. In other cases, however, a careful investigation to prove the parasitism is necessary. A preliminary examination of the lesions with a lens is first made, followed by a careful microscopic examination of the sections of the diseased tissues. The general tendency is to look for the mycelium in the lumen of the cells, but the mycelium more often lies between the cells inter-cellularly than within the cells. Differential staining so as to differentiate the mycelium from the host tissue may sometimes be necessary.

Very often the symptoms of disease may become manifest in parts of the host plant remote from the precise region where the causal organism is located. This happens in the wilt diseases and root-rots. The necessity of subjecting all the tissues to a thorough examination under the microscope to locate the pathogen is thus obvious.

Where a pathogen is a facultative parasite, it has to be brought into pure culture before it can be further studied. For this purpose small pieces of diseased tissue, a microscopic examination of which has shown the presence of the fungus, are washed and surface-sterilized by using silver nitrate–sodium chloride solutions. The tissue is at first placed in the silver nitrate solution (1 : 100) for two minutes and then transferred to the sodium chloride solution (1 : 100) in order to remove the silver salt. It is then washed in sterile water and placed on agar media in a petri dish, the entire process being done as aseptically as possible. The dish is then incubated at a suitable temperature. The fungus appears on the substratum in a few days. Identification of the isolates then follows.

The mere presence of a fungus within the tissues of a diseased plant does not mean that it is the parasite. Its pathogenicity has to be tested and proved by infection experiments. In proving the pathogenicity of leaf-spotting fungi, healthy plants are raised in sterilized soil in pots. When the plants have put forth four to five leaves, a suspension of the spores of the particular fungus is sprayed

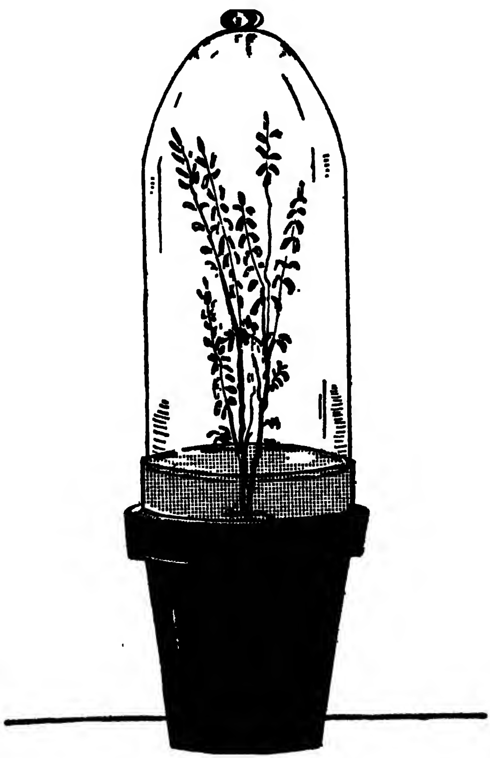


FIG. 37.—Incubation chamber using bell-jar.

on the leaves with an atomizer. The pots are then placed within a moist chamber so that the spores can germinate and germ-tubes enter the host. A bell-jar suitably placed over the plant serves as a good moist chamber. An incubation chamber made with a bell-jar is shown in Fig. 37. Lantern globes have sometimes been also used. The globes are placed over the plants, the upper opening being covered with a thin layer of cotton-wool held in place

with muslin cloth. Such lantern globes are very convenient for raising small plants (Fig. 38).

After a lapse of twenty-four or forty-eight hours, the plants are removed from the moist chambers and placed on the greenhouse bench, for by that time the spores will have germinated and the germ-tubes entered the host. If the fungus is the precise one that was responsible for the leaf-spot, the disease manifests itself within a few days. The period that elapses between the spraying of the host with

FIG. 38.—Incubation chamber using lantern globes.

the spores and the appearance of the disease is known as the **incubation period** of the disease. If the fungus fails to reproduce the precise symptoms of the disease, new isolations are made until the real pathogen is secured.

In conducting such pathogenicity tests a few precautions have to be taken. The tests should be conducted in greenhouses if they are available. The variety of the host plant must be, as a rule, the same as the one on which the disease had first appeared. This ensures that the test plants are not resistant, otherwise they may fail to take infection. Temperature and humidity conditions within the greenhouse must also be such as would favour the appearance of the

disease. Bright and direct sunlight must be avoided, as the spores may fail to germinate under such conditions. The soil must be kept well moistened to assist in maintaining the humidity.

Proving the parasitism of fungi causing wilts or root-rots is a very laborious process. As these diseases are soil-borne, the soil in which the host plants are to be raised has to be infested with the suspected pathogen. For this purpose the pathogen is grown in a medium such as a soil–maize meal mixture. Large quantities of the inoculum are thus obtained and mixed with the sterilized soil in a definite proportion. The soil is then potted. A couple of days later surface-sterilized seed is sown in the pots in the usual manner. The disease manifests itself in the plants, provided the right fungus has been used, after an incubation period which may extend from two weeks to two months. Such tests eliminate the non-pathogens. Adequate controls must always be provided in such work.

PARASITISM OF OBLIGATE PARASITES

The pathogenicity of the obligate parasites like the rusts, smuts, downy mildews and powdery mildews can, as already mentioned, be assumed because the nature of the pathogens admits of such assumptions. Nevertheless it is often necessary to conduct infection experiments in order to determine the incubation period of a disease or to study its complete symptomatology, or for determining the resistance of a particular variety of the host plant. Such experiments should, as far as possible, be done in dust- and spore-proof greenhouses.

Plants for this purpose are raised in pots containing sterilized soil, and when they put forth three or four leaves they are inoculated with spores taken from the rusted plants with a straight-edged scalpel and spread on the wetted leaves. If the plants to be inoculated have a waxy coating on the leaves, as in wheat, the leaves are drawn gently between the fingers. Atomizing the leaves with suspension of rust spores is not always advisable, for such immersion of the spores in water is detrimental to their normal germination. The plants for inoculation must be in the best growing condition, otherwise they may not take infection.

After the inoculated plants have been in the moist chambers for two to three days they are placed on the greenhouse benches, on which chambers made partly or wholly of muslin should be provided. Such chambers protect the cultures from stray spores. If the muslin

is occasionally sprayed with water the temperature within the chambers remains cool, and there is also an increase in humidity, both of which favour the appearance of the disease.

The pathogenicity of obligate parasites can also be tested on detached leaves. For this purpose the leaves are placed in water immediately upon removal from the plant, thoroughly washed in running water and then rinsed in several changes of sterilized water. They are then transferred to sterilized petri dishes containing just enough sterilized water to keep the air saturated. Spores taken directly from the rusted plants are then dusted on the leaves, the upper lid is replaced, and the dishes are kept in an incubator registering a favourable temperature for forty-eight hours. At the end of that period a 5 per cent sugar solution is gently added to the dishes. They are then replaced in the incubator. As the leaves obtain their carbohydrates directly from the solution, it is not necessary for them to be placed in light. The sugar solution is changed every two days when the dishes and the leaves are rinsed with sterilized water.

To minimize contamination in the cultures, extreme care must be exercised in preparing the dishes and in applying the inoculum. The same precision of aseptic technique must be employed that one would use in any careful mycological culture work. With due care the leaves can be kept in good condition for five to six weeks and infection more securely obtained.

LIFE-HISTORY STUDIES

Investigations on the life-histories of pathogenic fungi play an important rôle in plant pathological work. The mode of formation of spores, the different kinds of spores that are formed by a pathogen, the function of such spores, and the time of their formation, all have to be investigated. The morphology of the spores, both sexual and asexual, is useful in the identification of the fungus. Factors promoting the germination of the spores and the growth and development of the parasite yield important clues. The mode of transmission of the disease, the method of over-wintering or over-summering of the fungus and its host range, indicate weak links in the life-history of the parasite and furnish useful data in devising control measures.

REFERENCES

MAINS, E. B., "Notes on greenhouse culture methods used in rust investigations," *Proc. Indiana Acad. Sci.*, **1923**, 241–257 (1924).
MELHUS, I. E., "Culturing of parasitic fungi on the living host," *Phytopathology*, **2**, 197–203 (1912).
RAWLINS, T. E., *Phytopathological and Botanical Research Methods*, 156 pp. John Wiley & Sons, New York (1933).
RIKER, A. J., and RIKER, R. S., *Introduction to Research on Plant Diseases*, 115 pp. John Swift & Co., St. Louis (1936).
YARWOOD, C. E., "Detached leaf-culture," *Bot. Rev.*, **12**, 1–56 (1946).

CHAPTER V

CLASSIFICATION AND NAMING OF FUNGI

FUNGI form a division of Thallophyta—that is, plants without differentiation into roots, stems, leaves, etc.—and are divided into the following classes:

(1) **Myxomycetes** or slime moulds.
(2) **Schizomycetes** or bacteria.
(3) **Eumycetes** or true fungi.

There is a good deal of controversy regarding the position of Myxomycetes, which are often included in the animal kingdom and named **Mycetozoa**. Schizomycetes or bacteria are dealt with in the science of **Bacteriology**. Among bacteria there are several species which cause disease in plants. The Eumycetes or true fungi are subdivided into the following four classes:

Mycelium, if present, usually non-septate; if lacking, reproduction by budding; perfect state usually represented by oospores or zygospores; imperfect state by sporangiospores or their modifications . . .	**1. Phycomycetes**
Mycelium septate: if lacking, cells reproduced by budding:	
Perfect state present:	
Sexual state characterized by spores borne endogenously in asci	**2. Ascomycetes**
Sexual state characterized by spores exogenously produced on basidia . .	**3. Basidiomycetes**
Perfect state unknown	**4. Fungi imperfecti**

The classes are then divided into orders, families, genera and species. For practical purposes a **species** can be defined as any organism which represents the totality of individuals which, while showing recognizable and constant differences in structure from all other organisms, agree among themselves and with their progeny in all essential characters. A **genus** groups a number of species that show closer resemblance to each other than they do to others. The grouping of genera into **families** and of families into **orders** is based on the same principle.

Names are assigned to species, genera, families and orders. All these names are in Latin, as that was the universal language of educated people in Europe in the Middle Ages. Descriptions of plants are also in Latin, and this standardization of language has been of much help, for otherwise it would not have been possible to compare species whose diagnoses were in different languages, such as Japanese, Russian, Norwegian or Hindustani.

Until the middle of the eighteenth century the names assigned to plants were long and clumsy. Instead of being names, they were actually short descriptions, and it was difficult to remember them. In 1753 Carl Linnaeus, the Swedish botanist, proposed what is now known as the **binomial system of nomenclature** in his book *Species Plantarum*. According to this system every plant bears two names, the first being that of the genus to which it belongs, and the second its own specific name. The generic name is a Latin noun, and the specific name is adjectival or possessive, agreeing with the substantive in gender and case. Generic and specific names should not be very long or difficult to pronounce (like *Stereogloeocystidium subsanguinolentum*). They should, if possible, indicate the affinities or analogies of the genus or some properties of the species. Species, genera and families are sometimes named in honour of well-known mycologists. In *Puccinia butleri* the generic name is in honour of T. Puccini, a Florentine physician and teacher, and the specific name is after Sir Edwin Butler, the mycologist who did pioneer work on the subject in India. Specific names may be derived from names of places—for example, *Polyporus calcuttensis* or *Ravenelia indica*—and in the case of parasitic fungi they may be derived from the generic names of the host plants—for example, *Scopella fici* or *Ravenelia acaciae-arabicae*. The names of families end, as a rule, in *-aceae*, as in Peronosporaceae, and of orders in *-ales* (sometimes in *-ineae*), as in Uredinales (or Uredineae). Names of higher rank end in *-etes*, as in Basidiomycetes. In all formal citations of the name of a fungus, the name of the investigator who gave the name, known as the **author** of the species or genus, is added at the end. Thus *Colletotrichum* Corda means the genus founded by Corda, and *Colletotrichum falcatum* Went signifies the species of *Colletotrichum* founded by Went. When a binomial is followed by the names of two authors, the first name being in parentheses—for example, *Coleosporium oldenlandiae* (Massee) Butler—the name in brackets is the name of the author who first proposed the name, and the

second, outside the brackets, that of the author who transferred the species to another genus or changed its rank. The name *Uredo oldenlandiae* was proposed by Massee for a rust on *Oldenlandia aspera*; but Butler discovered its perfect state and transferred it to *Coleosporium*, and hence *Coleosporium oldenlandiae* (Massee) Butler. The earlier name is called a **synonym** of the latter.

Botanical and therefore mycological nomenclature is very complicated, and a proper understanding of it requires much experience in taxonomic work. International congresses of botanists have been held from time to time to frame rules that govern nomenclature so that there may be international accord among botanists. The first Congress was held in Paris in 1867 and the second in Vienna in 1905. Rules governing the nomenclature of plants were framed and passed at these Congresses, but it was not until the third Congress met at Brussels in 1910 that a few Rules for the nomenclature of the fungi were framed. These Rules have been examined and amended at Congresses held later, at Ithaca, U.S.A.; Cambridge, England; and Amsterdam, Holland. Until 1910 the nomenclature of fungi was supposed to start with Linnaeus, but in that year other starting dates for various cryptogams were decided upon. For fungi the starting dates are as follows :

Myxomycetes	1753. Linnaeus, *Species Plantarum*.
Fungi :	
Ustilaginales, Uredinales and Gasteromycetes	1801. Persoon, *Synopsis methodica fungorum*.
Other groups of fungi	1821–1832. Fries, *Systema mycologicum*.

Thus in rusts, smuts and Gasteromycetes, any name given to a genus by a botanist prior to the starting date—that is, 1801—is not valid. Only the name accepted or given by Persoon and included by him in his *Synopsis* is valid. For fungi belonging to the other groups the names accepted or given by Fries in his *Systema* are alone valid, those assigned before that date and not accepted by him being invalid. As for fungi discovered after those dates, the earliest valid names given to them by later mycologists are the correct names. In the case of polymorphic forms, the earliest name of the perfect state, provided it has been validly given, is the one to apply. The perfect state is the **ascus** in the Ascomycetes, the **teliospore** in the Uredinales, the **chlamydospore** in the Ustilaginales, and the **basidium** in the Basidiomycetes.

REFERENCES

BISBY, G. R., *An Introduction to the Taxonomy and Nomenclature of Fungi*, 117 pp. Imperial Mycological Institute, Kew (1944).

BRIQUET, J. A., *International Rules of Botanical Nomenclature*, 3rd ed. Gustav Fischer, Jena, Germany (1935).

HITCHCOCK, A. S., *Methods of Descriptive Botany*, 327 pp. John Wiley & Sons, New York (1925).

CHAPTER VI

PHYCOMYCETES

THE Phycomycetes are the lowest class of fungi, and include both aquatic and land forms. In the lower forms the mycelium is poorly developed, but in the higher forms it shows better development. Hyphae never form strands or tissues, and the thallus ranges in structure from isolated cells in the lower families to a richly branched mycelium in the families higher up in the class. Vegetative mycelium is as a rule unseptate, and the living parts form a continuous multinuclear cell. Septa appear at the time of formation of reproductive organs and in the old mycelium.

The characteristic asexual reproduction of this class is by the formation of sporangia inside which the zoospores are fashioned. In the land forms, however, there is a gradual transition, the sporangia themselves taking on the function of conidia. Sexual reproduction is by means of gametes or gametangia which may be isogamous or heterogamous. Phycomycetes are divided into two sub-classes as follows:

Gametangia dissimilar; perfect state represented by the oospores; imperfect state by zoosporangia germinating by the production of zoospores, or less commonly functioning directly as conidia .	1. **Oomycetes**
Gametangia morphologically similar; perfect state represented by zygospores; imperfect state by sporangiospores, modified sporangia functioning as conidia or by true conidia	2. **Zygomycetes**

OOMYCETES

The lowest members of the Oomycetes are aquatic saprophytes or parasites on water plants, especially the algae. Transition to a terrestrial habit takes place through amphibious forms, which are saprophytes in moist soil or facultative parasites on seedlings causing damping-off or blights. The higher forms have acquired a wholly terrestrial habit and obligate parasitism on higher plants.

In the lower forms the vegetative body is a single cell, which may be naked or provided with a membrane from the very beginning.

In the higher forms the mycelium is well developed and hyphae are adapted to an independent existence, so that hyphal fragments are able to grow into new individuals. The mycelium is, as already stated, coenocytic, but septa may be formed for delimiting reproductive organs or in old mycelium.

In the simpler forms reproduction is by means of zoospores which arise either in sporangia or in resting spores. In the higher forms the sporangia develop at the ends of sporangiophores, which may be branched or unbranched. The sporangiophores may proliferate—that is, grow through the base of the sporangium—and a new sporangium may arise beyond its predecessor. The number of zoospores that are formed in the sporangium depends on the number of nuclei that have chanced to flow into the sac from the thallus

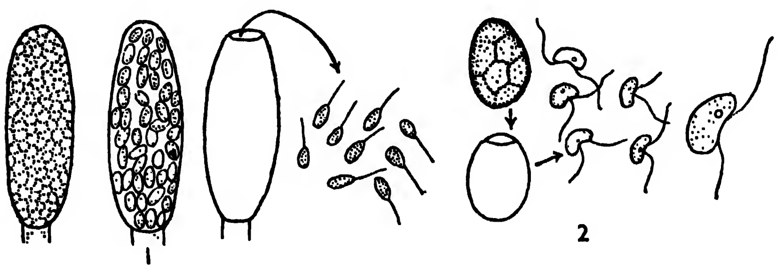


FIG. 39.—*1* Sporangia and ejection of monoflagellate zoospores (after Heald); *2* Sporangia showing cleavage and ejection of biflagellate zoospores (after Heald).

below. As sporangia mature, cleavage planes are formed within the protoplasm in an indefinite manner, turning the protoplasm into uninucleate pieces which round up and then become zoospores (Fig. 39). In the Oomycetes the cleavage furrows proceed outwards from a large central vacuole, but in the Zygomycetes they arise at the periphery and proceed inwards. There are, however, exceptions.

In *Pythium* cleavage may not, in some species, take place within the sporangium. Instead a vesicle is formed at the apex of the sporangium, into which the protoplasm moves; there cleavage takes place and zoospores are formed. When zoospores are formed within the sporangium itself, they escape through an opening in the sporangial wall, which is usually formed at the apex (Fig. 10). If they are developed in a vesicle (Fig. 44, *5*), the vesicle disintegrates and the zoospores escape. For a time the zoospores are biflagellate (Fig. 44, *6*) and motile, after which they become encysted by a wall.

Later they germinate by putting out germ-tubes and form a mycelium. In some species zoospores have two periods of motility, a rest period intervening; this phenomenon is known as **diplanetism.**

As development proceeds and forms take to a land habit, zoospore formation gradually degenerates and the function of the zoospores is assumed by the sporangium itself, which thus becomes a conidium. Transition forms can be found in the genus *Phytophthora*, whose sporangia produce zoospores at lower temperatures but act as conidia at higher ones. Germination of sporangia by means of germ-tubes

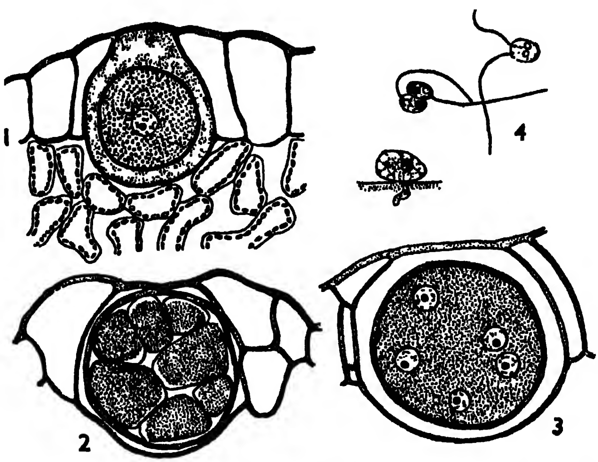


FIG. 40.—Summer sporangia and resting sporangia of *Synchytrium*, showing fusion of zoospores (gametes) and germination of zygote (*1*, *2* and *3* after Smith, *4* after Curtis).

is known as **direct germination**, and by the formation of zoospores as **indirect germination.**

As a change in the function of the sporangium takes place, a gradual increase in complexity of the sporangiophores becomes evident. As a sporangium which could give rise to numerous zoospores itself becomes a conidium, provision for the abundant formation of sporangia is made by their formation in chains or on multiple branches which the sporangiophores form. Whereas in *Pythium* the sporangiophore could hardly be differentiated from the rest of the mycelium, it can be easily made out in *Phytophthora*, and in *Peronospora* it is not only well developed, but also profusely branched. What is lost by the suppression of zoospores is made up in this manner.

Sexual reproduction. In the simplest forms of this sub-class a zoospore is a potential gamete, for in *Synchytrium endobioticum*, for example, it has been found that zoospores sometimes swim towards other zoospores and conjugate in pairs, and thus assume the rôle of gametes (Fig. 40, *4*). The fused cell moves for a time, comes to rest, and later infects the cells of the host. As several sporangia liberate their contents at the same time, it is probable that the conjugating zoospores are derived from different sporangia. The nuclei within the fused cell conjugate and form a zygote and pass

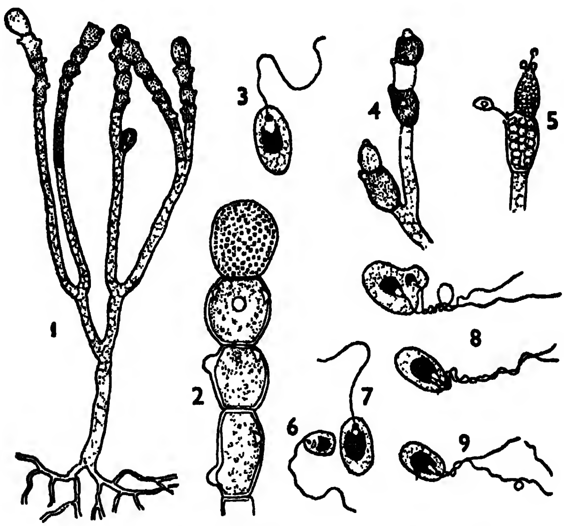


FIG. 41.—*Allomyces arbuscula* : *1* thallus ; *2* thallus with sporangia ; *3* zoospore ; *4* young sex organs ; *5* liberation of gametes ; *6* male gamete ; *7* female gamete ; *8* gametic union ; *9* motile gamete. (*1* and *2* after Smith, *3* to *9* after Kniep).

into a resting stage. In spring the nucleus divides meiotically, followed later by repeated mitotic divisions of nuclei (Fig. 40).

While the gametes are motile isogametes in *Synchytrium endobioticum*, they are non-motile heterogametes in *Olpidiopsis*.

Higher up in this sub-class sexual reproduction is typically heterogamous and, while gametic copulation is known, gametangial copulation is the rule; the male gametangium is the **antheridium** and the female the **oogonium**. The product of their union is the **zygote**. Gametes may be uni- or bi-flagellate, or both of them may be without flagella (**aplanogametes**). When heterogamy is

due to flagellated gametes it is known as **anisogamous heterogamy.** Heterogamy may also take place between a motile male gamete and a large non-motile female gamete, but more often the male and female organs are gametangia and are non-motile (Fig. 42).

Anisogamous heterogamy has been observed in the genus *Allomyces* (Fig. 41). Here the antheridia and oogonia are borne in short catenulate series on the same branch, one alternating with the other, and distinguishable from each other by the relative density of their protoplasts. Gametes are formed within them by progressive cleavage, and uniflagellate zoogametes escape through a pore in the oogonial or antheridial walls. The female gametes are twice the size of the male gametes (Fig. 41), and fusion takes place between them while they are still motile. The zygote is biflagellate, and it continues to swim for a time, but it soon settles down, and germinates within a short time.

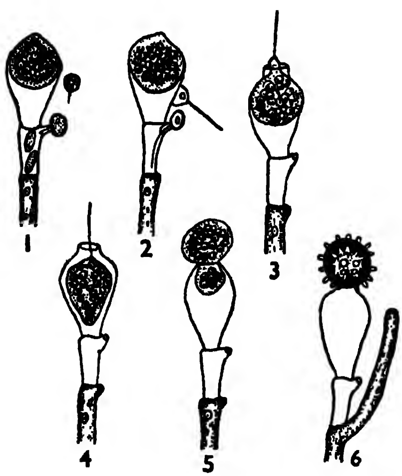


FIG. 42.—*Monoblepharis*. oogonium on top and male gamete below; *2* male gamete crawling into the oogonium; *3* and *4* union of male gamete and oogonium; *5* and *6* zygote formation (after Cornu and Woronin).

In *Monoblepharis* the male gametes alone are motile. The oogonium is a terminal enlargement in some species, with an uninucleate protoplast from the very beginning. The cell immediately below is the antheridium, which shows no swelling and contains five to six nuclei, each of which becomes the nucleus of the antherozoid. A small lateral beak is formed in the antheridium from which the antherozoids emerge (Fig. 42). This antherozoid swims to an oogonium, and then crawls in an amoeboid manner over the oogonial wall until the pore is reached, through which it effects entry and fuses with the egg. Very soon a thick zygote-wall is secreted and the two nuclei also fuse. The zygote may take several months to mature, during which time a reduction division of the fusion nucleus is stated to take place and four daughter nuclei are formed. At the time of germination the wall

of the zygote cracks and the hyphal outgrowth emerges in the usual manner.

In the higher forms where copulation between antheridia and oogonia takes place directly, the oogonium consists of homogeneous protoplasm to begin with; but this later contracts to form a large spherical naked body within the oogonium, which is known as the **oosphere.** It lies free and is surrounded by some left-over protoplasmic material of lighter consistency—the **periplasm.** After fertilization, the periplasm helps in the formation of the oospore-wall. The oosphere is, at first, multinucleate, but as a result of disintegration of all nuclei but one, it usually becomes uninucleate. Multinucleate oospheres occur in some species of *Cystopus.* There

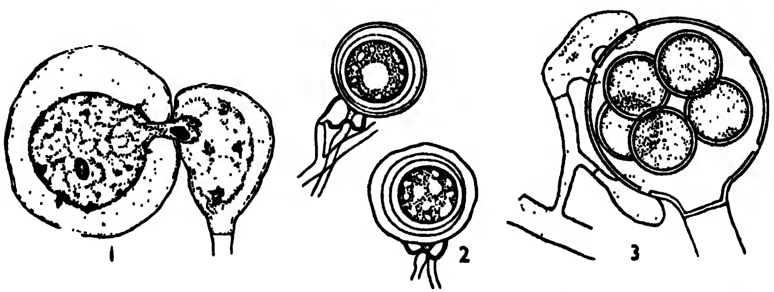


FIG. 43.—*1* Paragynous antheridium of *Pythium aphanidermatum* (after Edson); *2* amphigynous antheridia of *Phytophthora* (after Dastur); *3* oospore of *Saprolegnia* with multiple oospheres being fertilized by antheridia (after Coker).

is usually a single oosphere in an oogonium, but in the Saprolegniaceae more than one oosphere in an oogonium are known (Fig. 43, *3*).

Antheridia develop singly at the tips of slender hyphae and grow towards and become applied to the oogonia, into which they send delicate, filamentous outgrowths—the **fertilization tubes.** This tube penetrates the oogonial wall, pierces the oosphere, ruptures and discharges its contents. When more than one oosphere occurs in the oogonium, the fertilization tube may either branch or several antheridia may get themselves attached to the oogonium and send tubes into it. In some Saprolegniales, antheridia are not formed and oospores develop parthenogenetically into **parthenospores.**

When antheridia are formed on the stalk of the oogonia or a branch arising from it, they are called **androgynous.** If they develop on independent branches, they are called **diclinous.** The

antheridium is applied to the side of the oogonium, but in some species of *Phytophthora* the oogonium grows through the antheridial branch, which then surrounds the base of the oogonium. The former type of fertilization with androgynous or diclinous antheridia is known as **paragynous**, and the latter as **amphigynous** fertilization (Fig. 43, *1* and *2*).

Classification. The sub-class Oomycetes is divided into eight orders: (1) Chytridiales, (2) Blastocladiales, (3) Monoblepharidales, (4) Plasmodiophorales, (5) Saprolegniales, (6) Leptomitales, (7) Lagenidiales, and (8) Peronosporales. Species that are parasitic on plants of economic importance occur, mostly, in the first- and the last-named orders. The following families are of importance in plant pathology:

PERONOSPORALES

Sporangiophores little differentiated from vegetative hyphae; usually intracellular and without haustoria . . . . . **1. Pythiaceae**

Sporangiophores specialized. Mycelium intercellular and provided with haustoria:

- Sporangia in chains on clavate sporangiophores, in dense sori beneath the host epidermis; haustoria globose . . **2. Albuginaceae**
- Sporangia borne singly or in clusters on branched, rarely clavate sporangiophores which emerge through stomata, and transformed into conidia; haustoria various . **3. Peronosporaceae**

PYTHIACEAE

This family, which consists of aquatic, amphibious and terrestrial species, is transitional in character in so far as habitat is concerned. Several species are parasitic on flowering plants, those belonging to the genera *Pythium* and *Phytophthora* being the most important.

PYTHIUM

Species belonging to the genus *Pythium* are aquatic or amphibious in character, the latter living in moist soil, where some of them cause damping-off or root-rot of seedlings. The mycelium is freely branched and coenocytic, and asexual reproduction is by means of zoospores which, as a rule, are biflagellate and are produced in sporangia. Two types of sporangia are formed. In the first type, characteristic of some species, sporangia are elongate with irregular, twisted branches whose diameter is the same as that of the hyphae

bearing them. In the second type, characteristic of the rest of the species, sporangia have a definite shape, and their diameter is greater than that of the hyphae on which they are borne. A well-differentiated sporangiophore is, however, unknown in either case. A transverse septum to set off the sporangium from the rest of the hypha is present. As a rule zoospores are formed in vesicles. A vesicle may be formed at the apex of the sporangium, like a bladder, into which the protoplasm from the sporangium is emptied and the zoospores are fashioned and from which they later escape. Or the vesicle may be within the sporangium itself, which, after the formation of the zoospores, slowly emerges out of the sporangium (Fig. 48) and allows the zoospores to escape. In some species there may not be a vesicle, and the zoospores may develop within the sporangium and then escape through a pore at the apex.

Sexual reproduction is oogamous. The oogonium receives at the time of its development twelve or more nuclei, and the antheridium three or more. However, at the time of fertilization the oosphere has only a single nucleus, the rest having migrated to the periplasm. When the fertilization tube from the antheridium enters it, one male nucleus passes down the tube and enters the oosphere, but the two nuclei fuse only after the oospore gets enveloped by a thick wall.

Damping-off of Tobacco Seedlings (*Nicotiana tabacum* L.)

Damping-off is a very common seedling disease, and affects many crops in India. It is of widespread occurrence in tobacco seed-beds, where it does much damage. Several fungi are responsible for damping-off, but the most common are ***Pythium de Baryanum*** Hesse, ***Pythium aphanidermatum*** (Edson) Fitzpatrick and ***Pythium myriotylum*** Drechsler.

Damping-off appears at any stage of the growth of the seedlings; but usually manifests itself soon after the seeds have germinated, involving patches of plants in the seed-bed. All seedlings in the patch are killed, and the patch gradually enlarges. Some of the species of ***Pythium*** that cause damping-off may even attack adult plants. Affected seedlings are pale green and show a girdle of brown decaying cortex extending upwards and downwards from the ground-level. The seedlings then collapse and topple over owing to the weakening of the tissues at the base of the stem which, together with the leaves, becomes decomposed.

The most common species of *Pythium* responsible for damping-off is the classic *Pythium de Baryanum* (Fig. 44). It consists of much-branched, hyaline, coenocytic mycelium whose main strands are up to 5 μ in diameter, though the lateral ramifications are finer. The ends of the blunt terminal hyphae penetrate the cell-walls of the hypocotyl and ramify within and between the tissues of the cortical parenchyma. Sporangia and oospores are formed in the parenchymatic tissues of the host, especially in the cotyledons. Sporangia are terminal or intercalary, and may be 15–26 μ in size. They are spherical when terminal, and oval, barrel- or sausage-shaped when intercalary. A little before germination, a prominent beak is formed on the sporangium, followed by the formation of a thin-walled vesicle into which the sporangial contents are emptied (Fig. 44, *5*). The protoplasm is divided here into uninucleate pieces by cleavage, and up to twenty zoospores are formed within the vesicle. The zoospores are reniform, with two lateral flagella which arise from a hilum located on the concave side (Fig. 44, *6*). They are up to 8 μ in diameter, and germinate by the formation of germ-tubes.

Sexual reproduction is oogamous, oogonia being formed terminally at the ends of lateral branches or intercalarily. Antheridia are formed simultaneously, and one two or even three have been found attached to a single oogonium (Fig. 44, *9* to *13*). Whether all are functional is not yet known. The oogonia are 15–28 μ in diameter, while the oospores are 12–20 μ. The germination of oospores is by the formation of germ-tubes.

Moisture content of the soil and humidity of the air are prime factors that influence both infection and the subsequent course of the disease. The widespread occurrence of species of *Pythium* in cultivated soils shows that soil type is not a factor of importance. Plants are liable to severe infection in all soils that are poorly aerated and that are water-logged, especially if comparatively high temperatures prevail. Conditions which predispose seedlings to damping-off are, therefore, overcrowding, growth in damp localities, excess of water in the soil and presence of too much decaying vegetable debris. Care in the selection of sites is thus necessary. Avoidance of too thick sowing in the seed-beds aids in keeping down the disease.

Soil sterilization, using steam, dry heat or chemicals, is one of the best methods of controlling damping-off. The apparatus necessary for steam sterilization consists of a boiler, a pan and connecting hose. The boiler should have sufficient capacity to furnish a continuous

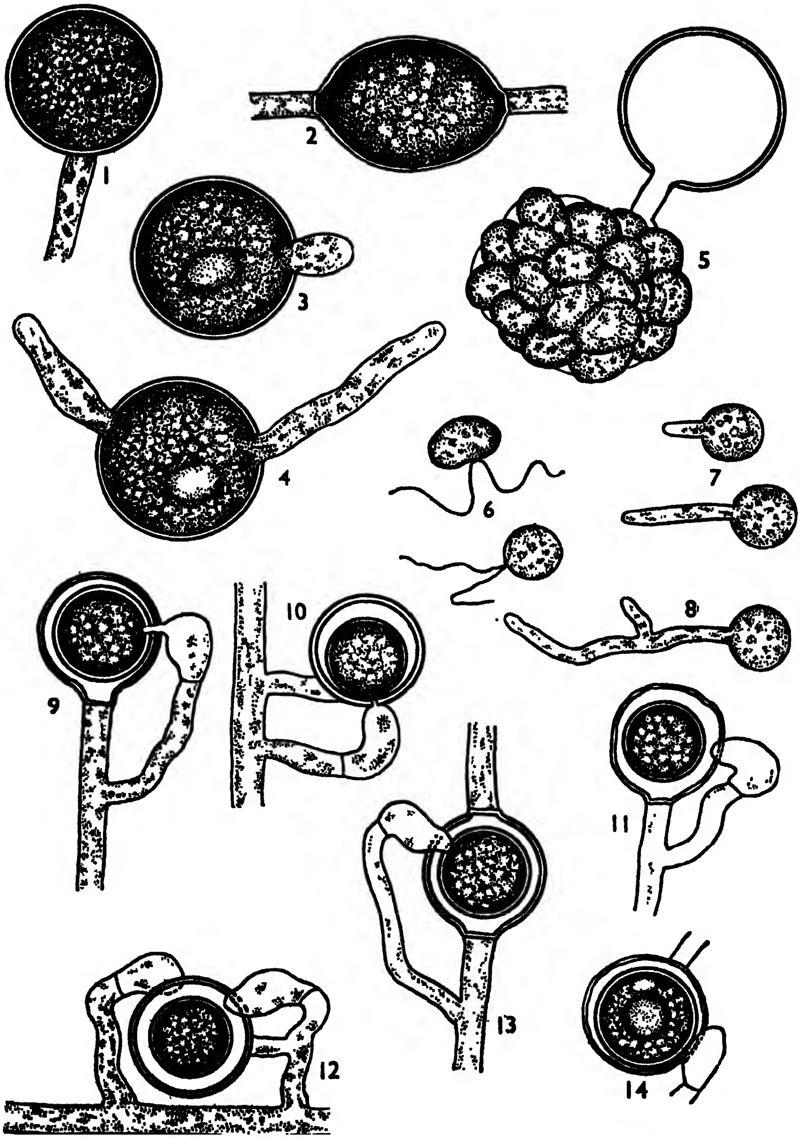


FIG. 44.—*Pythium de Baryanum* : *1* and *2* terminal and intercalary sporangia; *3* and *4* germination of sporangia by germ tubes; *5* germination of sporangium by formation of vesicle inside which zoospores are formed ; *6* motile biflagellate zoospores; *7* germination of zoospores; *9* to *13* antheridia and oogonia with developing oospores; *14* oogonium with mature oospore (after Buchholtz).

E

flow of steam to the pan at a minimum pressure of 80 lb. The pan may be of galvanized iron, and should be 9–12 feet long, 6–12 feet broad, and 8 inches deep. The edges of the pan should be sufficiently sharp to allow the pan to be forced down into the soil. Steaming should be continued for thirty minutes.

Sterilization by dry heat is usually accomplished by burning wood upon sites where the seed-beds are to be located. Soil that has been sterilized by steam or dry heat is more loose, friable and porous than unsterilized soil. It also remains free from weeds and grass.

Seed-bed soil can be sterilized by using formaldehyde, which should be diluted in the proportion of one part to fifty parts of water, and sprinkled over the loose soil in sufficient amount to soak it to a depth of at least 4 inches, which will mean the use of one gallon per 2 or 3 square feet of soil. Several days are required for the formaldehyde to evaporate before the seed can be sown in the soil. Two sprayings with Bordeaux mixture at the rate of one-half gallon per square foot, one before sowing the seed and the other a week after their germination, has also been reported to give satisfactory results.

Rhizome-Rot of Ginger (*Zingiber officinale* Rosc.)

Rhizome-rot or soft-rot of ginger is known to occur in almost all the areas where ginger is cultivated in India. When it appears in an epidemic form, the losses it causes are enormous, as the crop is a very lucrative one. *Pythium myriotylum* Drechsler, *Pythium aphanidermatum* (Eds.) Pitz., *Pythium monospermum* Pringsheim and *Pythium gracile* Schenk are some of the fungi that have been isolated from diseased plants, but so far only the parasitism of *Pythium myriotylum* and *Pythium aphanidermatum* (= *Pythium butleri*) has been actually tested and proved.

The disease manifests itself (Fig. 45) on the leaves, which turn slightly pale. Their tips turn yellow, and the yellowing gradually spreads down the leaf, which ultimately withers and dies. The whole shoot is finally affected, the foot of the plant and the rhizome also turning pale. The basal portion of the plant becomes watery and soft, and the rhizome, which is discoloured, gradually decomposes, forming a watery mass of putrifying tissue enclosed by the tough rind. Roots also rot in a similar manner, and the formation of rhizomes ceases.

The causal organism is actually found in the parts below ground

—that is, the rhizomes or roots. The mycelium of *Pythium myriotylum* is up to 8·5 μ in diameter, and forms numerous clavate, knob-like appressoria. Sporangia are terminal or intercalary, sometimes consisting of portions of outwardly differentiated filaments measuring up to 300 μ in length and 7 μ in diameter, with swollen, lobulate or digitate elements attached laterally (Fig. 46, *4* and *5*). Zoospores are

FIG. 45.—Soft rot of ginger rhizomes, healthy on left and diseased on right.

formed in the sporangium or within a vesicle formed at the apex of the sporangium into which the contents of the sporangial contents flow, become segmented, and finally form up to forty zoospores. The zoospores are reniform, biflagellate, mostly 10–12 μ in diameter, and germinate forming a single germ-tube.

Sexual reproduction is by the formation of oogonia and antheridia. The former are spherical or subspherical, smooth, thin-walled, terminal or intercalary, and have an average diameter of 28 μ. The

antheridia are typically diclinous, up to 30 μ long and 4–8 μ wide, and up to ten may be applied to an oogonium (Fig. 46, *1*). The oospores are slightly yellowish, subspherical, and 12–37 μ in diameter, but their mode of germination is not yet definitely known.

The disease is both soil-borne and seed-borne, 'seed' in this case being pieces of rhizomes. The choice of healthy seed-pieces for the prevention of the disease is thus an obvious necessity. As the mycelium and the fruiting bodies are within the seed-pieces, surface disinfection is not likely to yield any results. Rhizomes for use as seed must be obtained from areas where the disease does not occur.

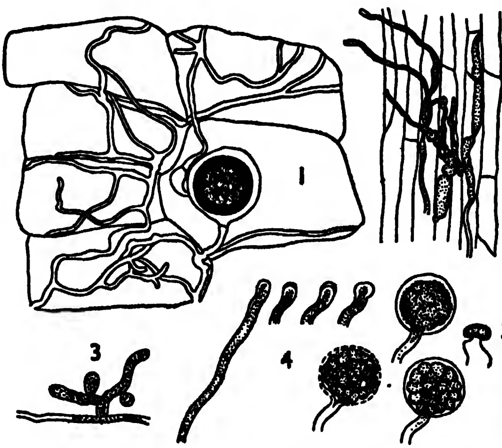


FIG. 46.—*Pythium myriotylum* : *1* part of rhizome of ginger showing mycelium with an oospore and antheridium; *2* mycelium in plant debris in water; *3* swollen lateral branch; *4* successive stages in zoospore formation; *5* a zoospore (after Butler).

In light, sandy soils with good drainage the disease can be effectively checked if water-logging is prevented. In some places spraying with Bordeaux mixture, at the rate of one-half gallon per square foot, once before sowing the seed-pieces, and then at two- or three-weekly intervals after their germination, has given good results. The concentration of the Bordeaux mixture for the first spray has to be strong. Trials with perenox, fermate, dithane and some of the newer non-metallic organic compounds may yield useful results.

Stem-Rot of Papaya (*Carica papaya* L.)

Stem-rot of papaya trees appears to be a widespread disease in India, Ceylon, Cuba, Hawaii and South Africa. It usually appears

in the rainy season, and the severity of the disease, it has been noted, depends directly on the severity of the rainfall.

The first indication of the disease is the appearance of spongy, water-soaked areas on the bark, at the region of the collar, just at and immediately above the soil line (Fig. 47). Simultaneously the terminal leaves begin to droop and wilt, becoming yellow and

FIG. 47.—*1* Foot of papaya tree affected by *Pythium aphanidermatum*; *2* stem of same affected by the same fungus.

falling off prematurely. If fruits are formed, they shrivel and drop to the ground.

The disease gradually spreads above and below the stem. Affected roots deteriorate, and some of them may be entirely destroyed. The entire stem becomes girdled at the base, and the patch may extend upwards to 2 feet or more. The tissues soften, and a copious exudation of latex takes place. Within the tissues the mycelium is both intra- and inter-cellular; as the disease advances the tissues become discoloured and rotten, and the decay extends to the cambium, and thence to the wood.

The disease is most common in trees that are two to three years old, being rare in younger trees. Affected trees may recover if dry weather intervenes. Even in cases of severe attack, the death of the

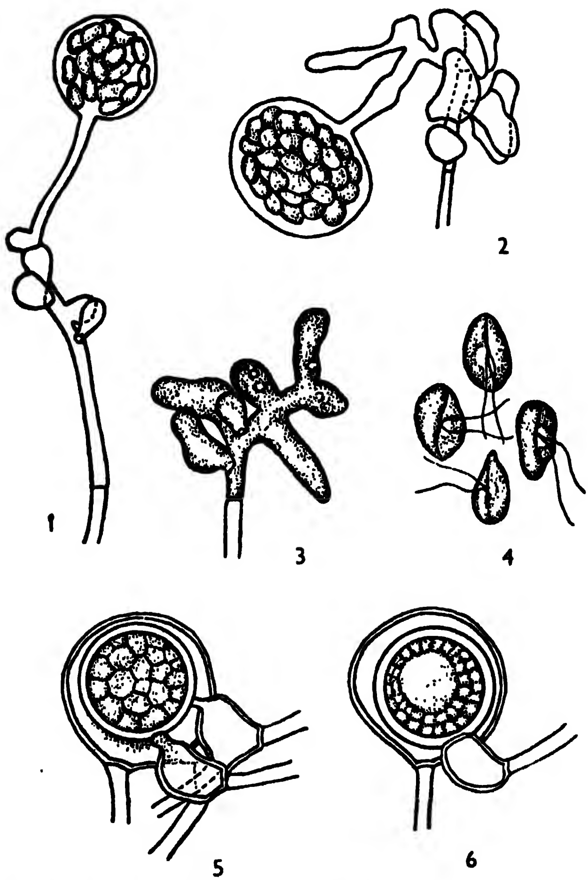


FIG. 48.—*Pythium aphanidermatum* : *1*, *2*, *3* sporangia and formation of zoospores in vesicles; *4* biflagellate zoospores; *5* and *6* oogonia and antheridia and the process of fertilization, paragynously (after Mathews).

tree is not brought about rapidly, and considerable time may elapse before it succumbs.

Several species of *Pythium* are reported to cause stem-rot of papaya, but in India *Pythium aphanidermatum* alone has been found to be responsible for stem-rot. The hyphae of this fungus are much branched, up to 8 μ in diameter, hyaline and non-septate.

Sporangia are in the form of lobulate outgrowths up to 500 μ in length and 20 μ in breadth (Fig. 48). At the time of germination a bladder-like vesicle is formed at the apex of the lobulate sporangium, into which the protoplasm flows. Later a large number of zoospores are formed within the vesicle. The zoospores are reniform, biflagellate, 9–11 μ in diameter, and move rapidly with a circular movement, after which they come to rest. Diplanetism is unknown.

The oogonia are smooth, spherical and usually terminal, ranging in diameter from 15 to 23 μ. The antheridia are broadly club-shaped, monoclinous, and one or two may be appressed against an oogonium. Oospores are thick-walled, do not completely fill the oogonium, and range in diameter from 17 to 19 μ. They germinate by the production of germ-tubes.

Stem-rot of papayas can be avoided if the plants are grown on well-drained land, where every effort should be made to avoid water-logging. If any plants are affected, they must be carefully uprooted and burnt, in order to prevent further spread. Replanting in the same place must be avoided. At the time of cultivation care must be taken to see that the base of the stem is not injured. No other direct methods of control have been tried.

Pythium aphanidermatum appears to be a cosmopolitan fungus of world-wide distribution. In India it attacks several varieties of cucurbits and also other crops. Another species, *Pythium graminicolum* Subramaniam, causes a foot-rot of wheat seedlings. The disease has not been properly investigated in India, but in the United States of America and Canada it is reported to attack wheat, barley and other cereals.

PHYTOPHTHORA

The mycelium in species of *Phytophthora* is profusely branched and non-septate when young, but septa are formed in old hyphae and at the time of formation of the reproductive bodies. The hyphae vary in diameter, and may sometimes become swollen, nodose or tuberculate. Chlamydospores which are formed in abundance are ovoid, non-papillate, hyaline to straw-coloured, and thick-walled. Asexual reproduction is by means of sporangia formed sympodially on the sporangiophores, which are only slightly distinct from the vegetative mycelium. In some species the sporangiophores resume growth through the base of the evacuated

sporangium. Sporangia are papillate and hyaline to light yellow. Zoospores are formed within the sporangium, and emerge through a pore in the sporangial wall in an amoeboid fashion. They are reniform and biflagellate, and before losing their flagella swarm about and then come to rest. Diplanetism is common. After they have come to rest and shed their flagella they become surrounded by a wall. Their germination is by the formation of germ-tubes.

Sexual reproduction is oogamous. Oogonia are spherical to pyriform, smooth, and hyaline to yellowish. Inside they have an oosphere which is free and which after fertilization develops into a smooth oospore. Fertilization is generally amphigynous, and the antheridial attachment persists below the oogonium.

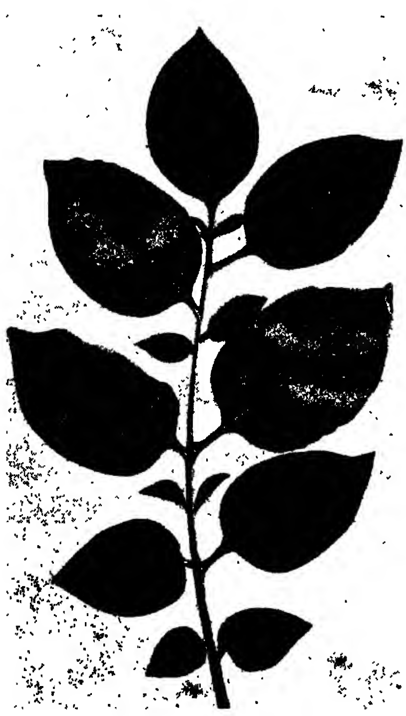


FIG. 49.—Potato leaves showing infection by late blight, *Phytophthora infestans*.

Late Blight of Potatoes
(*Solanum tuberosum* L.)

No plant disease has received such widespread interest as the late blight of potatoes. It is easily the most serious of all potato diseases, but in India epidemics of late blight do not occur in the plains, for the chief predisposing factors that render potato plants susceptible to the disease are absent during the period of their growth. In the hills, at elevations of 6000 feet and above, the disease does much damage, as the crop is grown in the rainy season, when the day temperatures are never above 22–23° C., being most favourable for its appearance.

The disease manifests itself only after the blossoming period, and the first signs (Fig. 49) are usually on the leaves as small black patches or purplish-black areas. If there is an accumulation of moisture from

favouring dew or rain, the sporangia germinate and the brownish-purple areas rapidly increase in size, involving the whole surface. If the affected leaves are examined carefully on a dewy morning, a delicate growth of the fungus is perceptible as a powdery bloom on the underside, but less often on the upper, where the diseased area borders the green. This aerial growth bears the sporangia which serve to carry the infection to healthy leaves. Infection soon spreads to the haulms, and the entire crown may fall over in a rotten pulp in a day or two. Within a week of the first appearance of the disease, all the plants may be stricken, especially if the weather is warm, muggy and moist, when ground fogs, heavy dews or rain continuously occur.

After the tops have been blighted, the underground parts, especially the tubers, are also affected. The upper sides of the tubers lying nearest the surface of the soil are first attacked. In the earliest stages the symptom is in the form of a slight brownish or purplish discoloration of the skin, and if the soil is moist the underlying tissues are softened. Later infection spreads inwards, so that the entire tuber turns brown and decays before harvest. In drier soils the progress of the disease is slower, and a dry-rot due to the drying-out of the dead cells may result. The surface of such tubers becomes slightly sunken and of a darker colour, and rusty-brown markings can be seen just below the skin. Dry-rot may or may not be in evidence at the time of harvesting, but it develops during the first month or two of storage. In dry weather, infections are limited, and the spots on the leaves remain small, brown and dry, while the haulms and the tubers may entirely escape the disease.

The fungus responsible for late blight was named *Botrytis infestans* by Montagne in 1845, but was transferred to *Peronospora* by de Bary in 1863. In 1876, however, he established the genus *Phytophthora* and transferred the fungus to that genus. The precise name of the fungus is therefore *Phytophthora infestans* (Mont.) de Bary.

The mycelium of *Phytophthora infestans* is branched, hyaline, non-septate and 4–8 μ in diameter. In older parts the mycelium is septate. It develops intercellularly in the parenchyma and forms haustoria, which alone enter the host cells. The haustoria are more common in the tubers, and can be seen as simple or branched, finger- or club-shaped, or roundish bodies, often surrounded by a sheath of cellulose formed by the host cells, presumably to shut off the parasite.

The sporangiophores are entirely aerial, and emerge through the stomata in little groups of four or five together, or sometimes through the epidermal cells. Sporangia are borne at the tips of the branches or the sporangiophores. After the formation of a sporangium, the branch continues to grow just below it and a new sporangium is formed. At each point where growth is renewed a nodular swelling is formed marking the place where the sporangia were borne (Fig. 50). There may be nine or ten such swellings in a branch.

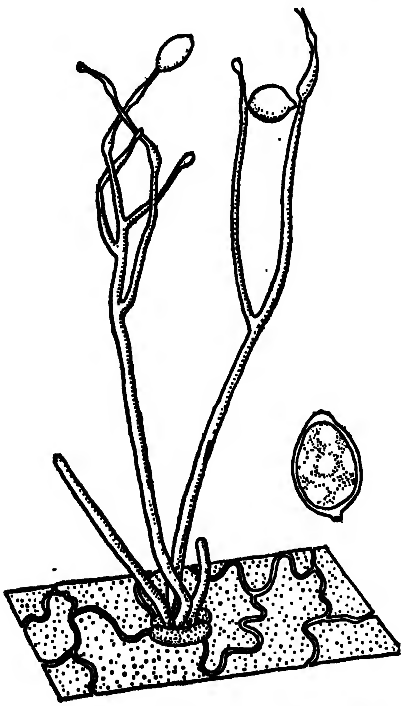


FIG. 50.—*Phytophthora infestans*: sporangiophore and sporangia of the fungus.

The sporangia are ovoid or lemon-shaped, hyaline, 22–32 μ long and 16–24 μ broad. They have an apiculate tip—the **papilla**. When the sporangium is mature, its protoplasmic contents become segmented into uninucleate pieces, each with a central vacuole. These develop into zoospores which escape later, when the papilla bursts. They rest in front of the opening for a while and then swim about, lose motility, drop their flagella, form a wall and germinate, pushing out a germ-tube. Some sporangia may germinate directly, forming a germ-tube at the apex.

Sexual reproduction is by means of oogonia and antheridia, the latter developing before the former. The oogonium when formed penetrates the antheridial cell from side to side, and fertilization is therefore amphigynous. The oogonium is pear-shaped to almost spherical and 31–46 μ in diameter. Its wall is smooth and reddish-brown. Oospores lie loosely within it and are about 30 μ in diameter. Parthenogenetic oospores are also known to occur.

Epidemics of late blight occur whenever environmental conditions are favourable for the formation and germination of both

sporangia and zoospores. It has been noted that a relative humidity of 100 per cent is necessary for abundant production of sporangia, none being formed at relative humidities of less than 90 per cent. Sporangia are produced in a saturated atmosphere at any temperature between 3° and 26° C., but the optimum temperature for rapidity and abundance of production is 21° C. The most favourable temperature for germination by zoospores is 12° C., and for germination by germ-tubes 21° C. Sporangia lose their viability rapidly at temperatures above 22° C. in moist air and less rapidly in dry air. Zoospores germinate at all temperatures between 3° and 22° C. and not at higher temperatures. Experiments have shown that the probability of infection at temperatures above 22° C. is much less both because of falling-off in germination and because of the slowness of growth of the germ-tubes and their penetration within the tissues.

The severity of infection is thus strictly governed by environmental conditions. In the plains of India, where potato is a winter crop, cool and moist weather is sometimes present and the disease may appear in a mild form, but as dry weather soon intervenes and relative humidity is as a rule low, late blight epidemics are very rare. On the hills potatoes are grown in summer, when both temperature and moisture are very favourable to the disease at the time of the growth of the crop. Late blight epidemics are therefore very common and frequent.

In order to check late blight, seed tubers should be obtained from areas where the disease does not occur, so as to eliminate direct infection. As such areas do exist in India, this is a feasible proposition. The best method which has so far given the greatest measure of control, is foliage spraying. Observations over a period of years have shown that spraying should start when the plants are 6–8 inches high. It should be repeated every ten or fifteen days, depending on the weather. If there is continuous rain, the spray may be washed off. In such cases spraying may have to be repeated immediately and also done more frequently. The spray must be delivered with considerable force in the form of a fine mist, so that not only the upper surface but the lower surface of the leaves and the haulms are completely enveloped by the protectant.

The best spray has been found to be Bordeaux mixture, but a spreader and a sticker have to be added to it to ensure that it spreads evenly on the foliage and does not get washed off. New fungicides, some made from non-metallic synthetic compounds, have been

favourably reported on from the United States of America, and among these fermate and dithane appear to have given the best results. They are sold in a ready-made concentrated form, and the ease of their preparation is another factor in their favour.

The search for potato varieties that are immune from or resistant to late blight has been going on for several years. Expeditions have been sent to Mexico, Chili, Peru and other countries on the slopes of the Andes by Russia, the United States and England to collect wild potato varieties, with a view to seeing if there are among them any that are resistant to late blight. One tuber-forming Mexican species, *Solanum demissum*, has shown complete resistance to late blight, and hybridization with commercial but susceptible varieties has been effected. Segregates that are resistant to the disease have been obtained. Considerable success in obtaining such resistant varieties for India has been attained at the Potato Breeding Station at Simla.

Breeding programmes for obtaining resistant varieties are likely to be complicated because of the existence of physiological specialization in *Phytophthora infestans*. Four races, distinguished by their reaction to differential hosts, have been observed in Germany, and such races may also occur in India.

Koleroga of Areca Palms (*Areca catechu* L.)

Koleroga (which means rot disease) is a serious disease of areca palms in western peninsular India. It has recently been reported from Assam, where this crop is also grown, but whether the disease is the same as koleroga is not yet precisely known. The disease is prevalent only in the rainy season, which extends from the beginning of June to the end of September, and the area infected by it comprises a tract with a rainfall varying from 75 to 300 inches during that period. Where the rainfall is less, the disease is scarce or negligible.

Koleroga usually makes its appearance two to three weeks after the beginning of the rains. The first sign of the disease is on the nuts (Fig. 51), on which a water-soaked area usually develops towards the base. The green colour of the shell becomes a darker green, the patch gradually spreads, and the nuts eventually lose their green colour and sheen. Attacked nuts soon begin to shed, and it is this abnormal dropping which signals the advent of the disease. Fallen nuts show on their surface a felty, whitish mycelial mass, and very soon the entire nut is enveloped by it. While the disease

is predominantly on the nuts, the tops of the trees are occasionally attacked, and as it advances on the crown of the plant, the trees may dry up, resulting in withering of the leaves and bunches. This does not happen very frequently, and the annual loss due to such deaths is not more than one per cent, but the loss due to the shedding of the nuts is enormous.

Heavy rainfall and constant moist condition of the atmosphere are undoubtedly the chief factors favouring koleroga. Abundance of light favours the emergence of zoospores, but continuous heavy rain may wash them off. It is obvious, therefore, that instead of continuous rain, an alternation of sunshine and rain is more conducive to the development of the disease. In areca-palm gardens the trees are as a rule closely planted, and the closer together the trees are, the less chance is there for a rapid drying-out when there is sunshine; the opportunities for the quick spread of the disease are therefore ideal.

FIG. 51.—Areca nuts affected by *Phytophthora arecae* (courtesy K. M. Thomas).

The fungus that causes koleroga is *Phytophthora arecae* (Coleman) Pethybridge. Its mycelium is coenocytic, and hyphae vary in diameter from 8 to 9 μ. The sporangiophores are irregularly branched and the sporangia differ in shape from pyriform to elliptical. They are 30–70 μ long and 26–43 μ broad. Four hours after their formation, the protoplasm within them becomes divided into uninucleate pieces which ultimately develop into zoospores. Zoospores emerge out of the sporangia in the presence of abundant light and humidity in the air. In fact, even for the development of sporangia good light appears to be necessary. Sexual reproduction is oogamous,

and antheridia are diclinous. The oogonia develop some time after the antheridia have formed. The oospores are smooth, spherical, amphigynous, and 23–36 μ in diameter. Their germination has not so far been observed.

The most effective method of controlling koleroga is by spraying. This, however, is somewhat difficult in the case of a crop like areca palms. The palms are rather slender, without branches and up to 70 feet in height. The bunches which are principally involved are near the crown, and only experienced labourers can climb the palms. At one time it was a routine practice to spray the trees repeatedly soon after the onset of the monsoon, but recent investigations conducted in the Bombay province have indicated improved methods of control. It is now known that areca palms harbour latent infection in their crowns during the non-monsoon period, and do not show any external symptoms of the disease. When the monsoon starts, lesions develop on the leaf-sheaths as minute specks surrounded by water-soaked areas. As the monsoon advances, these specks increase in size and a crop of sporangia is formed, which is then quickly disseminated. Such trees are thus a potent source of primary infection. Destruction of dead trees and removal of affected leaf-sheaths that harbour latent infection are therefore essential. Spraying such affected palms to localize infection has been found to be a good practice. Bordeaux mixture to which spreading and sticking agents have been added is very effective. In spite of the stickers, however, the spray may soon get washed off, and more frequent sprays to eliminate the foci of infection may thus be necessary.

Phytophthora Blight of *Colocasia*

Colocasia antiquorum Schott is an important vegetable crop both on account of its tender leaves and its succulent corms. The most serious disease affecting it is a blight of leaves and rot of corms due to *Phytophthora colocasiae* Rac. The disease first appears in August or September, and the earliest symptom is a small, dark, roundish speck on the leaves. These specks widen rapidly by centrifugal growth and become circular, oval or irregular. As the disease advances, a very large part of the leaf becomes involved. Drops of a yellow liquid ooze out from the leaf-surface, and the spot itself becomes roundish (Fig. 52). Later it dries and even forms a shot-hole. At the periphery of the spots which are zoned in different shades of brown, green and yellow, a delicate whitish haze due to

the sporangial stage of the fungus can be seen, if the leaves are examined carefully.

When there is excessive rainfall and high humidity, conditions for the spread of the disease are very favourable, and gradually the petioles, too, may become affected. They become so softened that they are unable to bear the weight of the large leaves, which then break off. Infection may extend to the inflorescence (Fig. 52), and in unusually wet years the corms may rot completely.

FIG. 52.—Leaf and flower of *Colocasia antiquorum* affected by *Phytophthora colocasiae* (after Butler).

The mycelium is unseptate, intercellular, and provided with longish, slender, unbranched haustoria (Fig. 53, *6*). Sporangiophores are formed on the surface of the leaves, and are up to 50 μ long, rather slender and exceedingly narrow at the tips. They bear, singly, the pear-shaped sporangia, which are 38–60 μ long and 18–26 μ broad (Fig. 53, *2*). As many as twenty zoospores, which are reniform and biflagellate, may be formed within a sporangium (Fig. 53, *1*). Direct germination of sporangia is also known. Chlamydospores are thick-walled, spherical and usually hyaline. The oospores are amphigynous, spherical, 20–28 μ in diameter, and lie free in the oogonium. The oogonia are yellowish and almost spherical, and antheridia persist at their base for a considerable period after the oospores are formed (Fig. 53, *3* to *5*).

Spraying with Bordeaux mixture gives complete control, but it should start some time before the disease appears in the fields. The precise time can be forecast if the disease has been under

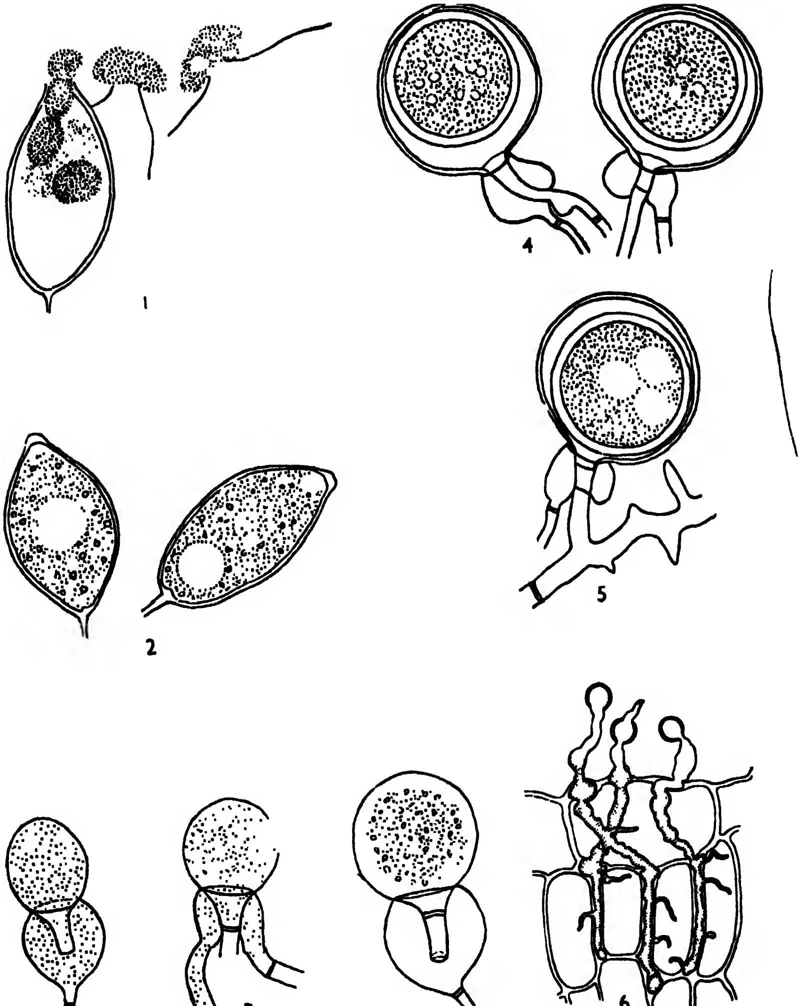


FIG. 53.—*1* Sporangium and zoospores of *Phytophthora colocasiae*; *2* sporangia; *3*, *4* and *5*, oogonia, antheridia and stages in fertilization; *6* penetration of leaves by the fungus (after Butler).

observation for a couple of years. The strength of the spray, the number of applications that should be given, and the use of wetting and sticking agents, have to be calculated, and what effect the chemicals have on the edible quality of the leaves has yet to be determined.

Seedling Blight of Castor (*Ricinus communis* L.)

A seedling blight of castor caused by *Phytophthora parasitica* Dastur is a common disease of the crop when it is grown in low-lying and badly drained fields, especially during the monsoon, when the

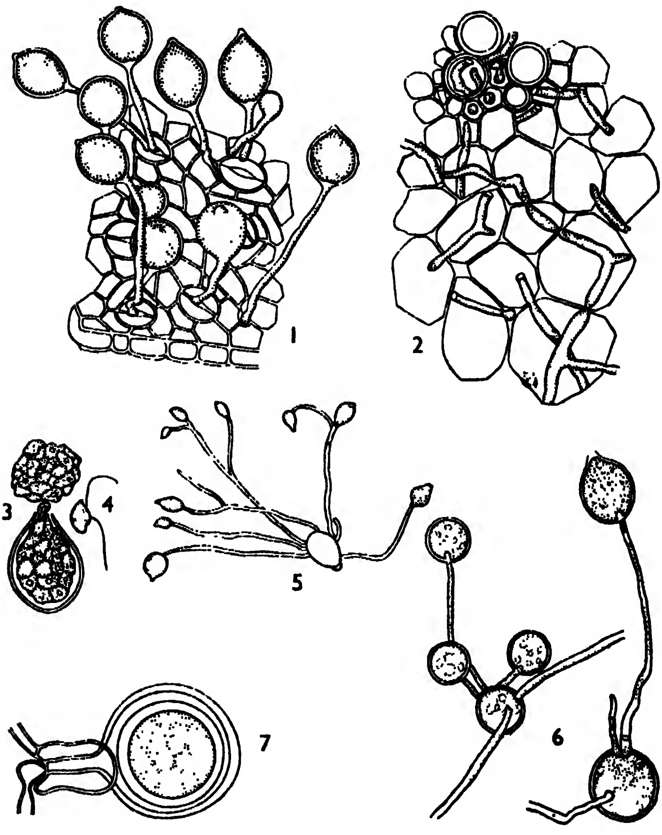


FIG. 54.—*1* Leaf surface of castor with sporangia; *2* hyphae in tissues of stem; *3* sporangia and ejection of zoospores; *4* zoospores; *5* a sporangium germinating with germ-tubes and secondary sporangia; *6* chlamydospore germinating and forming sporangium; *7* oospore with amphigynous antheridium (*1* and *2* after Butler, *3* to *7* after Dastur).

plants are 6–8 inches high. A roundish patch of dull green colour on both surfaces of the cotyledons is the first indication of blight, and this gradually spreads to the point of attachment of the leaf to the petiole, and the former hangs down in a rotting condition. If the

blight extends to the growing point and the stem, the damage caused is more severe. The true leaves may also be affected, but not much injury is caused at this time.

Phytophthora parasitica not only attacks castor seedlings, but several other plants as well, and its host range is therefore very

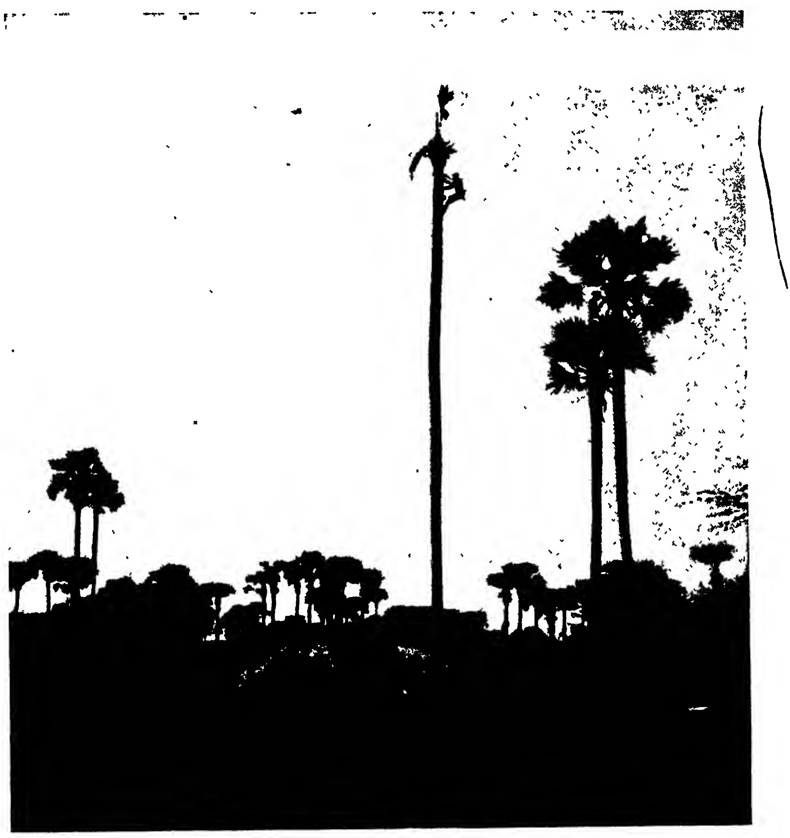


FIG. 55.—Bud-rot of toddy palm due to *Phytophthora palmivora*.

extensive. The mycelium is unseptate, inter- or intra-cellular, but there are no haustoria. All the leaf-tissues, including the fibro-vascular bundles, are invaded, but the fructifications are formed only on the surface of the leaves. The sporangiophores emerge through the stomata or by direct penetration of the epidermis between two adjacent cells (Fig. 54, *1*). They are slender, unbranched, 100–300 μ long, and bear sporangia singly at their tips. Sporangia are

hyaline, ovoid, papillate, and measure 25–50 μ in length and 20–40 μ in breadth. Mature sporangia when placed in water liberate zoospores, which are formed and liberated in the manner usual in this genus (Fig. 54, *3* and *4*).

Zoospores are reniform and biflagellate, and have a swarming movement. They come to rest from twenty minutes to two hours after discharge, and then begin to germinate. Direct germination of sporangia is also known. Both chlamydospores and oospores have been seen, though the latter are formed only in culture media. The oospores are amphigynous, 13–24 μ in diameter, round and hyaline. They do not completely fill the oogonium, which may be up to 27 μ in diameter with a thick, yellowish wall. The anteridium remains attached to the base of the oogonium for a long time (Fig. 54, *7*). Germination of the oospores has not so far been seen.

The parasite is soil-borne where it persists for long periods. I the crop is not grown in damp, low-lying localities, the disease may be completely avoided, and in that case other control measures are not necessary.

Among the other species of *Phytophthora* occurring in India, *Phytophthora palmivora* Butler is the most important. It causes a severe bud-rot of toddy palms (*Borassus flabellifer* L.) (Fig. 55) and coco-nut palms (*Cocos nucifera* L.) in southern India, where it has been brought under control by cutting down the affected trees and burning them.

ALBUGINACEAE

The Albuginaceae are a family of widespread distribution with a single genus, *Cystopus*, the species of which are obligate parasites on higher plants. The mycelium is unseptate, freely branched, and provided with globular, rarely knob-shaped, haustoria. It forms sori on the surface of the host, which resemble rust sori but they are creamy-white in colour (Fig. 22). They later burst and rupture the epidermis because of the pressure exerted by sporangia that are formed below.

Asexual reproduction is by means of sporangia which are borne on sporangiophores. Sporangiophores are short, hypodermal, clavate and unbranched, and stand in compact groups beneath the epidermis (Fig. 57). Sporangia are abstricted from the tips in basipetal order, and they remain attached in chains until the epidermis

is ruptured. They are hyaline, smooth, spherical, and produce kidney-shaped, biflagellate zoospores on germination. Zoospores swim about for a time, come to rest, drop the flagella, become surrounded by a cell-wall and germinate by putting forth germ tubes.

Sexuality is well developed in this family, and the sex organs are formed within the host tissues. In *Cystopus candidus* an inflated hyphal tip develops into an oogonium, a septum separating it from the thallus below. The cytoplasm within is at first uniformly vacuolate, and the nuclei are evenly distributed. Later the central portion becomes denser and is turned into an oosphere, and the peripheral portion into periplasm. The nuclei in the oosphere migrate, after a time, to the periphery into the periplasm and divide mitotically, the orientation of the spindles being such that one daughter nucleus lies in the oosphere and the other in the periplasm (Fig. 57, *3*). All but one nuclei disintegrate by the time the oosphere is ready to receive the male nucleus. Meanwhile the apical portion of the other hyphae lying near the oogonial hyphae becomes converted into small antheridia which are also cut off from the rest of the hypha by septa. Each antheridium contains several nuclei. When mature, the antheridia develop slender fertilization tubes which grow through the oogonial wall and the periplasm, and penetrate deeply into the oosphere. A single nucleus enters and fuses with the nucleus in the oosphere.

In one or two other species of *Cystopus* more than one nucleus remain functional and are fertilized by the entry of an equal number of male nuclei. The resulting oospores are thus multinucleate, and are known as **compound oospores.**

A thick wall, with three distinct layers, is formed around the oospores. The sculpturings on the surface of the epispore are characteristic of the different species and have diagnostic value (Fig. 57, *2*). When the oospores are mature, the nuclei within the simple oospore also divide until thirty-two nuclei are formed in each, after which the oospores over-winter or over-summer, as the case may be. They germinate in spring, when the nuclei divide again and again. More than a hundred biflagellate zoospores may thus be formed by a single oospore. The oospore wall then cracks, a thin vesicle is formed, and the zoospores are extruded into it in a mass (Fig. 57, *3*). Later, the vesicle disappears and the zoospores swim freely in all directions.

White Rust of Mustard (*Brassica campestris* L.)

White rust is a common disease of several cruciferous plants, such as cabbage, turnip, mustard and radish, and occurs throughout India. All parts of the host may be attacked with the exception of the roots. It produces white or creamy-yellow pustules of various sizes and shapes, and very often several of them coalesce to form patches. They are formed below the epidermis and are unbroken, but with the pressure of the sporangia from below they rupture the epidermis and appear as powdery masses on the surface of the leaves. The leaves are principally attacked, but they are not as a rule distorted, and the pustules appear only on the lower surface; in severe cases they may be present on both surfaces. In some other cruciferous hosts the leaves may become thickened, fleshy, pallid or inrolled, and when infection is intense there may even be a reduction in the size of the leaves, and the entire plant may become dwarfed.

FIG. 56.—Inflorescence of *Eruca sativa* affected by *Cystopus candidus*.

In some hosts the swellings on the stem are slight, but in others the entire stem may be uniformly swollen for a length of several inches. Lateral buds that are normally latent may proliferate, resulting in a bushy growth. When peduncles are attacked they become enormously swollen, but cases are not rare where the flowers alone are attacked (Fig. 56). Affected flowers show various discolorations and malformations; the petals may be turned into sepals and the stamens into leaf-like or carpelloid structures. They may sometimes be changed into thickened, club-shaped sterile bodies. Occasionally, in some hosts, the stamens are less affected, a part remaining fertile and the other part remaining sterile. Very often the pistil is hypertrophied into a large, conical, thick-walled sac or transformed into a

sterile carpellary leaf. The parasite stimulates cell activity, leading to an increase in cell-size, cell-division, and formation of chlorophyll and starch at places where none is usually formed. The mycelium is strictly intercellular, knob-shaped haustoria helping in the absorption of food.

After growing vigorously at the expense of the host, branches from the internal mycelium collect beneath the epidermis and send haustoria into the leaf parenchyma. The sporangiophores arise from

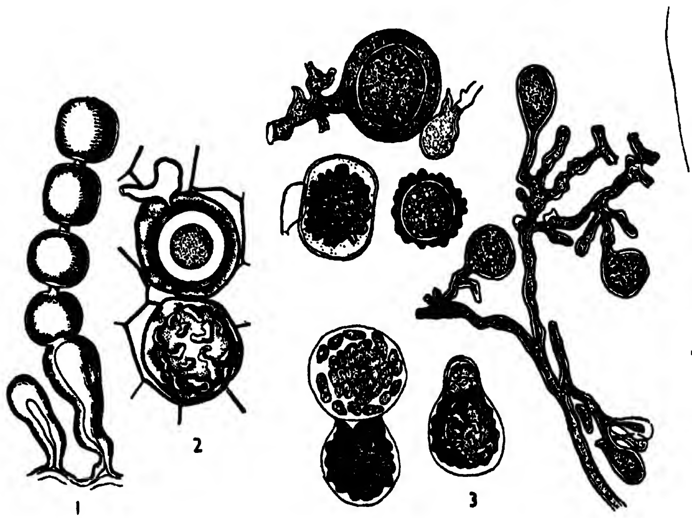


FIG. 57.—*Cystopus candidus*: *1* Sporangia and sporangiophore of *Cystopus candidus*; *2* oospores of same (both after Berlese); *3* stages in the fertilization and formation of oospores and germination of oospores (after de Bary).

these hyphae. They are free from each other laterally and slightly thick-walled at the base. The epidermis at this stage undergoes a change and the cells swell owing to the thickening and gelatinization of the wall. With the advent of moist weather the epidermis bursts, exposing the sporangial bed. The sporangia are formed in basipetal chains and measure 12–18 μ in diameter. Oospores are formed only in some hosts, and their formation is conditioned by certain factors of environment. They are globular, provided with a tuberculate brown epispore, and 40–55 μ in diameter. Their germination takes place after a long period of rest and is by the formation of zoospores

(Fig. 57, *3*). The rest period can be shortened if they are chilled at 4° C. for a week.

The precise conditions of environment that favour the disease—the mode of over-summering or over-wintering and of dissemination—have not been investigated in India, and the disease has not received the attention that it should. No recommendations regarding the methods of control can therefore be made. In Japan it has been found that there is a certain degree of parasitic specialization in the fungus. The relative susceptibility or resistance of the different varieties of mustard to this disease has not yet been determined. White rust is prevalent every year in a mild form, and severe epiphytotics are rare, and the losses caused are therefore not very high.

PERONOSPORACEAE

This family consists of species that are obligate parasites on higher plants. Its mycelium is coenocytic and strictly intercellular. Haustoria form a prominent feature and are globular, finger-like or filamentous (Fig. 5). The fructifications are not formed within the tissues of the host, as in *Cystopus*, but on the surface. Sporangiophores arise from an endophytic mycelium and protrude into the air. They are club-shaped, thick, and dichotomously branched in some genera. The branches arise in some cases at acute angles and in others at right angles. Sporangia are borne singly at the tips, and are pear-shaped, deciduous and disseminated by wind. In genera with a simpler type of sporangiophores, sporangia germinate by the formation of zoospores, but in those in which the sporangiophores are more complex they germinate directly, assuming the rôle of conididia. In *Sclerospora* and *Plasmopara* both direct and indirect types of germination are known. Sexual organs are formed within the tissues, and antheridia are paragynous, but whether they arise from the same hypha or not is not precisely known. Oospores are spherical, with strongly developed and sculptured epispore, and germinate by the formation of germ-tubes. Germination by the formation of zoospores occurs in *Plasmopara*.

Diseases produced by species belonging to this family are known as **downy mildews**. The mycelium here is wholly endophytic, whereas in the **powdery mildews**, due to species of Erysiphaceae, it is ectophytic. There are some exceptions. Of the six genera in the family, the following three are the most important from the plant-pathological point of view :

Conidiophores simple, or monopodially or dichotomously branched:
- Conidiophore fugacious, stout, sparingly branched; oospore permanently united to the wall of the oogonium . . . . **Sclerospora**
- Conidiophore persistent, slender, usually freely branched; oospore free from the wall of the oogonium . . . . **Plasmopara**

Conidiophore dichotomously branched; conidia germinating by a germ-tube from the side . . **Peronospora**

SCLEROSPORA

In this genus the mycelium is much branched, and haustoria are small and vescular. The conidiophores are erect, solitary or in groups of two or three. They are fugaceous, short and sparsely branched. Conidia are elliptical, hyaline and smooth, and germinate by forming zoospores when they are true sporangia, or by germ-tubes when they are true conidia. The oospores are globose, intramycelial, with a brown and irregularly wrinkled epispore, and permanently united to the persistent wall of the oogonium. There is an extraordinary preponderance of oospores, the conidial formation being not very common. Conidia are as a rule formed in the early hours of the morning, when there is an abundance of dew and cool temperature. In some species—*Sclerospora philippinensis*, for example—oospores have not yet been observed.

Green Ear Disease of Bajra (*Pennisetum typhoides* Stapf)

This is a very common disease which occurs wherever bajra is grown in India. At one time it was considered to be unimportant, but it has now been found to do much damage to the crop. It is known on jowar in Africa, and the fungus causing this disease—*Sclerospora graminicola* (Saccardo) Schroeter—attacks several species of *Setaria* in Europe, the United States and Japan.

The principal symptom is produced in the inflorescence, where the solid spicate ear is transformed wholly or in part into a loose head composed of small, twisted, leaf-like structures (Fig. 58) which give it a green appearance. The bristles of the spikelets become hypertrophied and variously contorted, and the glumes become enlarged and turn green. Instead of a single spikelet, two may be formed on a pedicel, and an increase in the number of florets in a spikelet is not uncommon. The stamens may be converted into leaf-like bodies (Fig. 59) or they may even be entirely suppressed.

The pistil rarely develops in severely attacked plants, and is usually replaced by samll, leafy shoots or horn-like growths. These changes greatly modify the appearance of the ear.

When leaves are attacked, their green colour is changed, wholly or in part, to white and later to brown. The cholorotic areas occur as long streaks and extend over the entire length of the leaves. On the underside they are covered by the whitish down of sporangia, which are formed in abundance on dewy nights. The leaves may become distorted by being twisted and crinkled, and tend to split into shreds. Shredding of the leaves is more common in jowar downy mildew,

FIG. 58.—Ear of bajra (*Pennisetum typhoides*) deformed by downy mildew.

FIG. 59.—*1* Proliferation of spikelets of bajra; *2* leaf-like stamen from same (after Butler).

caused by *Sclerospora sorghi*. In *Setaria italica*, which is attacked by the same fungus that causes the downy mildew of bajra, shredding is also very common.

The mycelium is strictly intercellular and provided with haustoria. In the leaves it is restricted to the mesophyll tissues, rarely penetrating the epidermal layer. The fibro-vascular bundles are, however, never attacked. The leaf cells are induced to multiply, and both the xylem and phloem elements also multiply, so that there is an increase in the size of the bundles. The chlorophyll from the assimilating cells gradually disappears, so that the leaves assume an etiolated and chlorotic appearance.

Sporangiophores arise from the internal mycelium and develop in the air-space below the stomata. They then emerge through the stomata singly or in groups. The sporangiophores are hyaline, broad, non-septate, unbranched in the lower part, but a few short, thick branches are formed dichotomously at the extreme end (Fig. 60, *1*). The tips of the branches are slightly swollen and the sporangia are borne on swellings. Sporangia are hyaline, broadly elliptic, with a papilla at the free end (Fig. 60, *3*). Their wall is smooth, and they measure 13–34 μ in length and 12–23 μ in breadth. They germinate by liberating numerous zoospores, the optimum temperatures for their germination being 18–23° C. Zoospores are

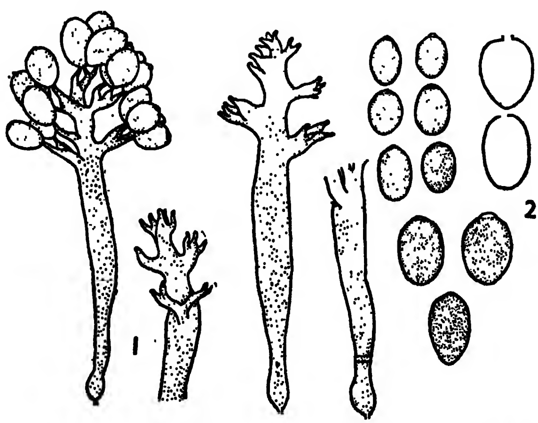


FIG. 60.—*Sclerospora graminicola*: *1* Sporangiophores; *2* sporangia.

irregularly reniform and biflagellate. Soon after emission they swim for a while, come to rest, and then germinate, forming germ-tubes.

The oosporic stage is the more predominant stage in *Sclerospora graminicola*. It develops later in the season, and is confined to the areas that appear brown. In the leafy structures formed in the inflorescence and in the leaf-blades, oospores are formed in the mesophyll, but an extensive destruction of the tissues with consequent shredding of the leaves into masses of tangled fibres, so characteristic of the Italian millet attacked by it, or of jowar attacked by *Sclerospora sorghi*, is not common. The oospores do not occur in rows, but are scattered. They are spherical, with a smooth wall of even thickness around which the oogonial-wall persists. The latter is tawny in colour, irregularly thickened, and gives the oospores

an angular shape. The oospores vary in diameter from 26 to 42 μ and have a mean diameter of 35 μ. They do not germinate immediately, but have a prolonged rest period. When they do germinate, they put forth germ-tubes which are hyaline and non-septate (Fig. 61). The optimum temperature for their germination is between 20 and 25° C.

The green ear disease is primarily a soil-borne disease. The oospores that have fallen to the ground with the debris of the plant, germinate when favourable conditions appear. Such conditions are: an abundant air supply highly charged with oxygen, a low soil moisture content, and a favourable temperature, between 20° and 25° C. In soils with a high moisture content the seedlings germinate quickly and emerge much earlier, and thus escape infection. In addition to this infection from the soil, there is secondary and local infection due to attack by zoospores. Zoospores are produced in large numbers nocturnally, and quickly spread the disease. Oospores produced on the Italian millet retain their viability for at least five years, and this may be so in the case of the bajra strain also.

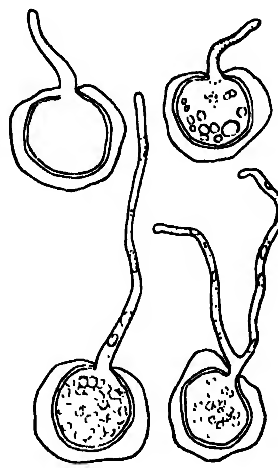


FIG. 61.—Germinating oospores of same (after Miura).

Investigations carried out at Poona have indicated that there are physiologic races in *Sclerospora graminicola* which can be differentiated on the basis of their parasitism on differential hosts. One race is restricted to bajra, and the other attacks species of *Setaria*.

Control of green ear disease, which is at first soil-borne and then air-borne, can only be by the development of resistant varieties. There is little hope of controlling it by other means. The reaction of different varieties to attack by the fungus, however, has yet to be determined.

Downy Mildew of Jowar (*Sorghum vulgare* Pers.)

Downy mildew of jowar is prevalent throughout peninsular India, where this crop is grown. In the Central Provinces and Northern India the disease is unknown. The causal organism was

at one time considered to be a variety of *Sclerospora graminicola*, but has now been raised to specific rank under the name of *Sclerospora sorghi* Weston and Uppal.

The disease is soil-borne and systemic. The oospores that lie about in the soil germinate at about the time the crop is sown, and the germ-tubes attack the seedlings. Affected seedlings have pale yellow and narrow leaves which are covered with a fine down consisting of the conidial stage. As the seedlings grow, white streaks appear on both the surfaces of the leaves. The tissues then tear along the streaks, causing shredding, which is the most characteristic symptom (Fig. 63, *1*). About this time the white streaks turn brown owing to the formation of oospores which are embedded in the tissues of the leaves. The plants remain stunted and sterile. Those that have escaped attack in the seedling stage are affected when they are two to three months old, by conidia formed on diseased plants. In such cases the leaves, especially those at the top, turn white. Irregular, brown or yellow streaks then appear and oospores develop in large numbers in the tissues. Affected plants are rarely fertile.

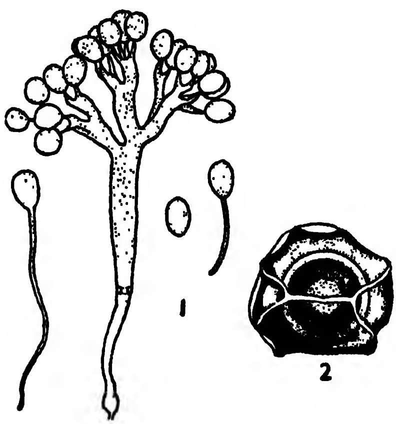


FIG. 62.—*Sclerospora sorghi* : *1* sporangiophore and sporangia; *2* oospore.

If the ears are produced at all, they are small and provided with only a few grains. The teratological malformations described in the bajra disease are not produced. While considerable shredding is the rule, in some plants it may not take place, and the oospores may not be formed. Instead, conidia are produced in abundance on both sides of the leaves.

The mycelial characters of *Sclerospora sorghi* do not differ from those of *Sclerospora graminicola*. Asexual reproduction is by means of conidia, which on germination give rise, however, to germ-tubes and not to zoospores (Fig. 62, *1*). They are almost suborbicular to spherical, and lack an apical papilla of dehiscence, for which there is no need, as zoospores are lacking. Conidia are 15–29 μ in diameter, and thus smaller than those of *Sclerospora graminicola*.

The oosporic characters are similar to those of the latter fungus (Fig. 62).

The precise conditions that promote epidemics have not yet been ascertained, and a detailed investigation of the disease is desirable. Some years ago it was observed that in a plot on the agricultural farm at Dharwar, which had received excess farm-yard manure, downy mildew appeared in a most severe form, whereas in the neighbouring plots with normal fertilizer or less, the incidence of

FIG. 63.—*1* Shredding of leaves of jowar due to attack by downy mildew; *2* shredding of leaves of maize due to attack by *Sclerospora philippinensis*.

disease was slight. As in the green ear disease of bajra, effective control can be effected only through the development of resistant varieties.

PLASMOPARA

The mycelium of the members of this genus is typically coenocytic and branched. It is strictly intercellular, and provided with simple haustoria. The sporangiophores are erect, solitary or fasciculate, and emerge, as a rule, through the stomata. They are monopodially branched, the main and secondary branches arising at right angles to the axis. They are not, therefore, truly dichotomous.

The ultimate branches are apically obtuse. The sporangia are globose to ovoid, hyaline, papillate, usually germinating by means of zoospores, but direct germination is not unknown. The oospores are yellowish-brown, their epispore being wrinkled and in a few species reticulate. The oogonial wall is persistent, as in *Sclerospora*, but is not fused with the epispore, as in the latter. At the time of germination, the oospore wall cracks open and a germ-tube protrudes,

FIG. 64.—Downy mildew of grape due to *Plasmopara viticola*.

at the end of which a sporangium is cut off, which germinates by forming zoospores.

Downy Mildew of Grape (*Vitis vinifera* L.)

Downy mildew is a common disease of the grape-vines, and has been reported from several parts of India, though not in a severely epidemic form. All the succulent parts of the vines are attacked, leading to a partial or total destruction of the foliage, dwarfing and killing of the shoots, and rotting and cracking of the berries.

The first manifestation of the disease is the appearance on the upper surface of the leaves of small, greenish-yellow spots, the margins of which blend into the darker green of the leaf. The spots increase in size, coalesce with the others and later turn brown. If the air is moist, frost-like patches of white fungous filaments appear on the lower side of the leaves (Fig. 64). Eventually they dry up, become brittle and are shed. Extensive shedding leads to shrivelled

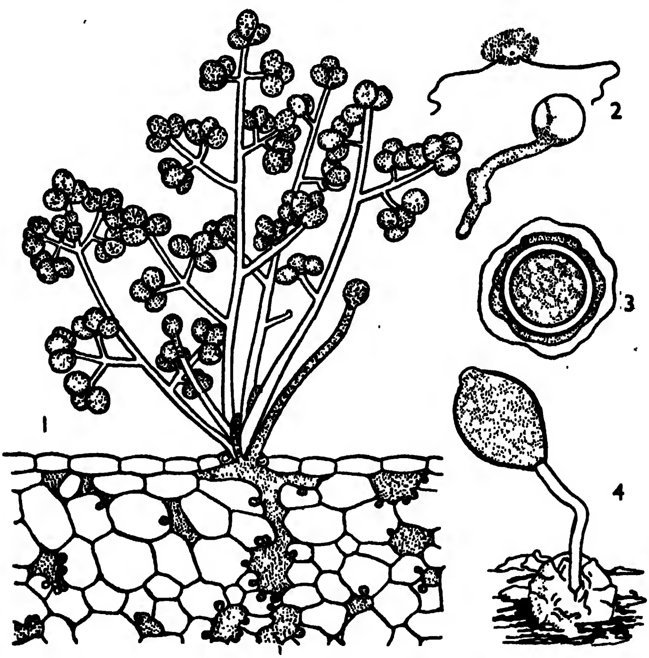


FIG. 65.—*Plasmopara viticola* : *1* Sporangiophores and sporangia emerging out of the grape leaves, intercellular mycelium with haustoria ; *2* zoospores and their germination ; *3* oospore ; and *4* germination of the oospore (after Melhus).

bunches, and the crop may be rendered worthless. On the shoots, petioles and tendrils, the affected parts bear a water-soaked, spongy appearance, and attacked berries rot in large numbers.

The mycelium is intercellular with vesicular haustoria. The contents of the parasitized cells are turned brown by the fungus. Sporangiophores, which are branched, emerge through the stomata. They bear myriads of sporangia, which are 15–31 μ long and 11–18 μ broad and which rapidly disseminate the fungus (Fig. 65). Their germination is as a rule by the formation of zoospores. Oospores

are 25–35 μ in diameter, with a roughed epispore. They germinate after a period of rest by producing germ-tubes on which sporangia are borne and which germinate in the usual manner and initiate the disease.

The fungus causing downy mildew in grapes was originally named *Botrytis viticola* by Berkeley and Curtis, but de Bary determined its true relationship to the Peronosporaceae and named it *Peronospora viticola*. It was later transferred to *Plasmopara*, which genus was founded by Schroeter in 1886, and its present name is therefore *Plasmopara viticola* (Berk. & Curt.) Berlese & de Toni.

Climatic conditions primarily influence the occurrence and spread of this downy mildew. As the most favourable temperature for the germination of sporangia is between 10° and 23° C., cool temperatures are necessary for infection. Humid and cloudy conditions are also essential for the germination of sporangia and zoospores, and for facilitating their dissemination. Sporangiophores and sporangia may not be formed if the atmospheric conditions remain dry. Continued hot and dry weather with plenty of sunshine operates against this disease, and the chances of its becoming epidemic in that event are slight. As the entry of the germ-tubes into the leaves is mainly through the open stomata, factors unfavourable to their opening prevent infection. The disease is carried over from year to year by means of oospores. Sanitary measures such as cutting the primary source of infection and preventing, by deep cultivation and ploughing, the germination of oospores are desirable practices. Removing and burning all diseased leaves, shoots and berries that may contain hibernating oospores helps in preventing epidemics.

In regions where grape culture is very important and downy mildew occurs every year, the disease has been effectively controlled by spraying the vines with Bordeaux mixture. If the precise environmental factors that promote its epidemics are known, it is possible to forecast the appearance of the disease, and spraying should start about a week prior to the probable date of its appearance. The vines are usually sprayed when the shoots are 6–8 inches high, again when they are about to blossom, and finally when the fruit is about to change colour. Six or eight sprays are stated to be necessary, but more may be desirable if there are frequent rains during the period. Local conditions determine, therefore, the time of application of the spray. Bordeaux mixture, which is extensively

used for controlling grape downy mildew, was in fact first invented to combat this serious disease in the environs of Bordeaux in France.

PERONOSPORA

The highest expression of parasitism has been attained in this genus, and all its species are aggressive parasites. The mycelium is well developed and strictly intercellular. Haustoria are short and knob-like (Fig. 66, *4*) or filamentous and more or less branched (Fig. 5, right). Conidiophores consist of an erect trunk which is branched from two to ten times, the branches being more or less reflexed and at acute angles (Fig. 12, *1*). As the spores are true conidia and not sporangia, for they never germinate forming zoospores, every device has been adopted to increase their number. Conidia are hyaline to slightly tinted, and they do not have a papilla. Germination takes place from an indeterminate point on the side of the conidia by means of a germ-tube. Oospores are globose or ellipsoidal, reticulate, tuberculate or smooth, and germinate forming germ-tubes.

Downy Mildew of Peas (*Pisum sativum* L.)

Downy mildew is a common disease of peas in the Indo-Gangetic plains, and may occur in the other parts of India also. It is widespread in Europe and North America, but is generally considered unimportant.

The symptoms become noticeable at the time the third and fourth leaves are expanding. Localized yellow to brown spots manifest themselves on the upper surface of the leaflets and stipules, and ultimately the infected tissue may die and turn brown. Concurrently with these symptoms on the upper surface, the corresponding areas of the lower surface of the leaves become yellow, and are soon covered with a whitish, downy coating which changes to a light violet-grey colour. The infected areas vary from irregular spots to elongated blotches. On the pods the disease is first noticed during the flat-pod stage as pale green, more or less elliptical blotches on the sides, or more irregular, elongated lesions along the dorsal sutures of the pods. Gradually the blotches darken to a bright brown colour, mottled with light green islands. Seeds adjacent to the infected tissues, especially those under the lesions along the dorsal suture, are generally aborted and considerably reduced in size. Systematically infected plants are very stunted, some of the parts being swollen and showing more or less rosette-like appearance.

The pathogen rarely produces conidia on the pods, though they are abundantly produced as a dull, mouldy growth over the entire surface of the leaflets and the stipules, which become reduced in size and curl downwards at the edges. Soon after the conidia have formed, the affected parts wither and die and, where the entire plant is involved, death usually ensues before the flowering stage is reached.

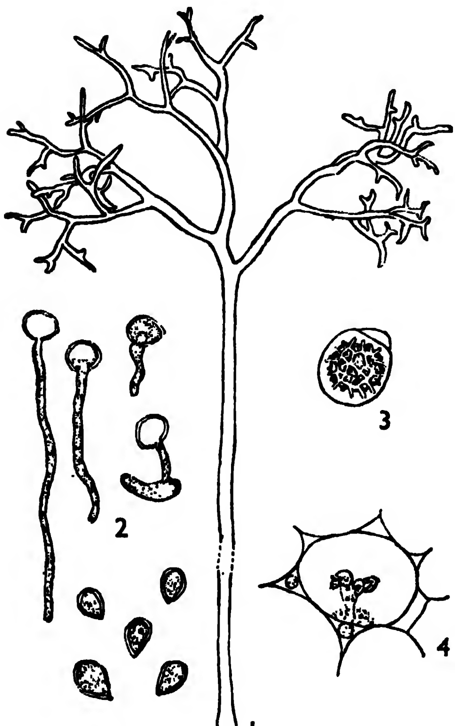


FIG. 66.—*Peronospora pisi*: *1* conidiophore; *2* germinating conidia; and, *3* oospores; also showing *4* host cell with haustorium (after Campbell).

The fungus which causes the downy mildew of peas is *Peronospora pisi* Sydow. It has a hyaline, intercellular mycelium which branches profusely. Finger-shaped or branched haustoria penetrate into the host tissue. Conidiophores, which arise in clusters, emerge through the stomata on the underside of the leaves. They are unbranched for two-thirds or more of their length, and bifurcate two to seven times at the apex, the ultimate branches diverging from each other at right angles (Fig. 66). Conidiophores may be up to 1·3 mm. long, and conidia are borne at the tips of the ultimate branches. Conidia are oval to elliptic, greenish-yellow or tinged with violet-purple, and 22–27 μ long and 15–19 μ broad.—They cannot stand desiccation and are short-lived. Germination is effected by the development of germ-tubes which are formed at their sides (Fig. 66, *2*). Oospores are embedded in the tissues of old and withered leaves or in the tissues of the pods (Fig. 66, *3*). They are almost spherical, greenish-yellow, 26–43 μ in diameter, and have a thick epispore with large reticulations. They lie singly within a large,

thin-walled oogonium which disappears after a time, and germinate after a period of rest, forming germ-tubes.

Two types of symptoms characterize pea downy mildew: one is due to systemic infection from the oospores, and the other to local infection. Experiments conducted in the United States have confirmed that contaminated soil is a source of infection, but whether the mycelium and the oospores which are found in the seed-coat also cause the primary and systemic infection has not yet been definitely proved. Moist, cool weather is conducive to the development of the disease, while warm, dry weather retards it. As desiccation of even fifteen minutes is fatal to the conidia, dry weather prevents its spread.

Spraying and dusting peas with fungicides against downy mildew appear to be the most likely methods of control, but in tests carried out in the United States they did not prove of much value under field conditions. Destruction of debris which may contain the oospores is a good practice, and rotation of two to three years is also recommended, by which time the oospores in the soil become inactivated.

This account of *Peronospora* cannot be closed without a reference to the downy mildew of cruciferous plants. The disease attacks the above-ground parts of turnip, radish, cabbage, cauliflower, and the oil-seed *Brassica* species. It is not, however, very common in India. The damage caused, when the disease has been noticed, has never been very serious. The fungus which is responsible causes purplish-brown spots on the underside of the leaves. These may remain small or enlarge considerably. On the upper side the lesions appear tan to yellow. When the sporophores emerge out of the stomata, usually on the lower side of the leaf, a typical mildewed appearance becomes manifest. Plants that are severely attacked may become predisposed to other diseases. The fungus causing this disease was formerly known as *Peronospora parasitica* (Pers.) de Bary (Fig. 12, *1*, *2*, *3*), but critical studies conducted by Gäumann have established that this is a composite species and that a large number of smaller morphological and biological species which are usually specialized on single host genera, and often on single host species, can be segregated. The fungus attacking *Brassica campestris* (sarson or mustard), for example, is named by him *Peronospora brassicae* Gäumann.

ZYGOMYCETES

This sub-class of Phycomycetes is of mycological rather than plant-pathological interest. Plant parasites are rare, but the family Entomophthoraceae is characterized by the pathogenicity of its species to insects. A large number of forms of this class are saprophytes, and among them are a few which have industrial uses. The aerial mycelium and the fruiting structures are very prominent, and the sub-class consists of the so-called moulds.

The members of this sub-class are wholly terrestrial with a well-developed, branched and coenocytic mycelium. In the older mycelium, or whenever the hyphae are damaged, or at the time of the formation of reproductive bodies, septa usually appear. The nutritive mycelium is embedded in the substratum, but the reproductive organs are, as a rule, aerial.

Several methods of reproduction have been observed in the Zygomycetes. Simple yeast-like sprouting occurs in a few forms, but asexual reproduction is the rule, and this is mainly through non-motile, endogenously produced spores known as **sporangiospores** or **aplanospores**, cut off in the sporangia. Sporangia are large, globose to pyriform and multi-spored. Inside the sporangia a prominent plane, shaped like a watch-glass, is laid in the cytoplasm, along the tip of the sporangiophore. This plane is smooth, cylindrical or pyriform, and persists even after the sporangial wall has degenerated. This structure is known as a **columella** (Fig. 67, *2*). The columella is not a protrusion of the basal septum of the sporangium into the sporangium. The formation of the aplanospores is more or less like that of zoospores. They have no flagella, and are therefore non-motile. In their formation, cleavage furrows within the protoplasm proceed from the periphery or the columella to the centre.

In the lower forms the sporangiophores are unbranched, but in the higher ones they are forked, racemose or corymbose. The gradual transition of the sporangium into a conidium can be traced in several cases. This tendency is first apparent when the size of the sporangium gradually diminishes and the number of aplanospores formed within is reduced. Ultimately the sporangium becomes a deciduous structure with three or four sporangiospores. To such a sporangium the name **sporangiolum** has been applied. When finally the sporangiolum becomes monospored, the change into a conidium is complete.

The most interesting case is that of *Choanephora*, where sporangia are, as a rule, formed when the fungus is poorly nourished. When the supply of nutrition is increased, only conidia are formed. It will be noted that the transition from sporangia to conidia parallels the *Pythium-Peronospora* series. There, the form and size of the sporangium are not reduced, nor is there a reduction in the number of zoospores that are formed, but only an inhibition in the formation of zoospores takes place so that the conidium is more or less an abnormality owing to unfavourable conditions. In the Zygomycetes, however, there is no inhibition in the formation of aplanospores, but a diminution in the size of the sporangiolum takes place until it eventually becomes equivalent to a conidium.

Sexual reproduction is of the isogamous type, both the mating organs being more or less alike (Fig. 67, *3*). When the time approaches, a protuberance arises on each one of any two neighbouring branches. These grow towards each other as a result of a contact or chemical stimulus. They grow in size and become the copulating branches known as **progametangia**. A transverse septum is laid in each progametangium, resulting in the formation of two cells: the basal cell is known as the **suspensor**, and the end one as the **gametangium**. After the gametangium has come into contact with a corresponding one on the other side, the wall between them is dissolved and the cell contents fuse. The product of this copulation process is the **zygospore**. The zygospore grows, envelopes itself with a new wall, and becomes the resting spore. The suspensors have a typical shape and are encrusted with a dark substance.

Zygospores were first observed in the Mucorales by Ehrenbergh in 1829. Their formation in some species is capricious, though in others, like *Sporidinia grandis*, they are invariably produced. In *Mucor mucedo* and *Rhizopus nigricans* zygospores are not formed if cultures are from a single aplanospore, but if a mass of mycelium from a culture which is not monosporic is used for the transfer, then zygospores appear in abundance about the point of inoculation, decreasing in number as growth widens. Examination of these cultures indicates that zygospores appear at the junction of certain mycelial colonies and not at others.

In 1904 Blakeslee announced that in *Mucor mucedo* and *Rhizopus nigricans* there are two physiological and sexually different strains or races which when grown apart produce only sporangia. When hyphae from the physiologically and sexually different mycelia are

allowed to come into contact, then they mate and form zygospores. As two different thalli are necessary for zygospore formation, he calls such species **heterothallic**. These mycelia with different sexual tendencies are morphologically indistinguishable, though a slight difference in the luxuriance of their growth can sometimes be distinguished. One strain he designates **plus** (+) and the other **minus** (—), but it is not possible to say which is male and which is female.

In species like *Sporidinia grandis* and *Mucor hiemalis*, however, zygospores are formed by the interaction of hyphae arising from the same aplanospore. These are termed **homothallic** by Blakeslee. The heterothallic condition is essentially similar to that in dioecious plants, excepting that, in fungi, there is no morphological difference between the two races. In *Sporidinia grandis* and some other similar species there is evidently no sexual differentiation in their thalli, and they are thus comparable to hermaphrodites of the higher plants.

Blakeslee who did considerable work on this phenomenon, found that the (+) race grows better on maltose than the (—) race and that the former has a greater capacity to reduce tellurium salts than the latter. He also discovered that if a (+) race of a heterothallic species is mated with the (—) race of *another* heterothallic species, imperfect hybridization takes place, resulting in the formation of imperfect zygospores. This enables the classification of sterile races of Mucor into (+) and (—) groups. In his studies on the germination of the zygospores of homothallic and heterothallic species, Blakeslee found that a heterothallic species like *Mucor mucedo* gives rise to **germ sporangia** in which all the aplanospores are either (+) or (—), segregation of sex having taken place at some point before the formation of aplanospores. Thus a single zygospore produces aplanospores of but one sort. In a few other heterothallic species, like *Phycomyces nitens*, he found that a single zygospore may produce both (+) and (—) aplanospores and even a few spores that are homothallic in their sexual tendencies. But the sexual character in such homothallic species is not stable, and the homothallic condition ultimately disappears.

Heterothallism has been found to be of common occurrence in fungi, and several facts that were formerly not very clear are explained in terms of this phenomenon. The formation of asci in several Ascomycetes, telia in rusts and basidia in the Eubasidiomycetes, is governed by heterothallism.

Formation of zygospores without a sexual act having taken place

between two physiologically different, homothallic or heterothallic mycelia is also known, and the zygote so formed is called an **azygospore.** The nuclear phenomena accompanying conjugation of gametangia and the maturation of zygospores and azygospores are not well understood. It is not known, for example, how many pairs of nuclei fuse in the zygote, but it is assumed that a reduction division takes place before germination starts.

Zygomycetes are divided into two orders, Mucorales and Entomophthorales. The species belonging to the former order are mostly saprophytes. The asexual spores are typically aplanospores, but the entire sporangium may function as a spore when it becomes a conidium. Sexual reproduction is by zygospores, whose outer wall is developed from the gametangia. In Entomophthorales the zygospores are free within the gametangial vesicle. Modification of sporangia into conidia is complete in this order. The conidia, which may be in chains, are discharged with force in some genera. Most of the species are parasites of insects, nematodes or protozoa. Seven families are at present recognized in Mucorales and three in Entomophthorales. Only three genera—*Rhizopus*, *Mucor* and *Empusa*, which are representative of this sub-class—are discussed below.

RHIZOPUS

Rhizopus nigricans Ehrenberg is the commonest mould and has been generally used for teaching purposes because of the large size of its sporangia, ease of culture on moist bread, and representative characters. It forms an abundant, soft, white cottony growth, and the plant body is a filamentous many-branched mycelium. Within the young hyphae is granular protoplasm containing many vacuoles of varying sizes, droplets of oil and glycogen. The protoplasm is in continuous movement, chiefly towards the tips of the different branches. In the older mycelium three types of hyphae occur. Those of the first sort anchor the plant by means of **rhizoids** or false roots (Fig. 67, *1*) to the substratum, which they also penetrate. They secrete enzymes which digest the foods. A second type of hyphae, usually larger than the rhizoids, grow almost parallel to and above the substrate for some distance and then bend downwards and produce another group of rhizoids. These are **stolons** or **runners.** Hyphae of a third type grow upward from the stolons at points where the rhizoids are formed, which are clusters of sporangiophores.

A young sporangiophore is full of protoplasm containing much

food and many nuclei. These migrate to the tip, which enlarges to form the sporangium. Later the food and the nuclei aggregate in the outer part of the enlarging sporangium, leaving the centre occupied by the protoplasm with many vacuoles and a few nuclei. Some of the vacuoles become arranged in a dome-shaped layer between the outer and denser protoplasm and the inner but less dense protoplasm. These vacuoles unite and form a large vacuole. A cleft separating the outer from the inner part of the sporangium is then

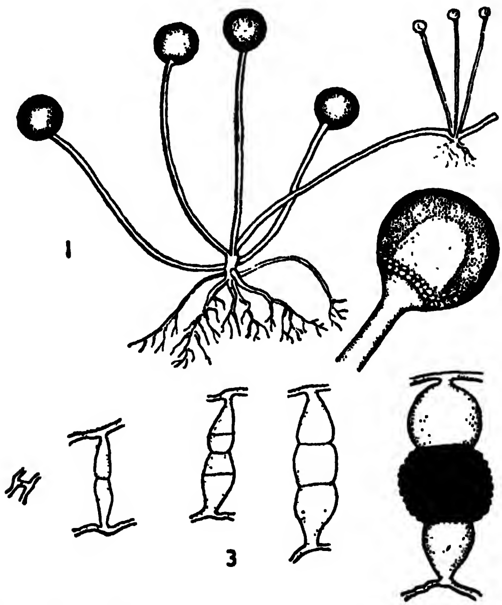


FIG. 67.—*Rhizopus nigricans* : *1* mycelium, rhizoids and sporangia ; *2* sporangium with columella ; *3* stages in the formation of zygospores (after de Bary).

formed, and a wall is secreted, which separates the dome-shaped central part of the sporangium, the columella, from the outer part, the spore-sac proper (Fig. 67, *2*). The plasma membrane in the spore-sac then becomes furrowed at various points both on the side next to the outer wall and on that next to the columella. The furrows cut into the protoplasm, branching and dividing the contents into small pieces of irregular shape. These small pieces of protoplasm, produced by this process of progressive cleavage, are the spore-initials. They become rounded, and each piece secretes a wall and becomes the aplanospore. The aplanospores are usually

uninucleate, but are without flagella. When the sporangial wall dries and becomes fragile, the slightest disturbance breaks it and the aplanospores are liberated. The columella persists as a dome-like structure.

Sexual reproduction takes place when two hyphae of (+) and (—) races respectively come into contact; a short progametangium is produced by each hypha at the point of contact. The terminal portion of each progametangium becomes swollen, and a transverse division occur within it. A cross-wall is secreted, the many-nucleate end cell being the **gametangium**, and the basal cell of the progametangium the **suspensor cell.** In time the walls between the two gametangia dissolve and they unite to form a zygospore (Fig. 67, *3*). Zygospores have thick walls and a rough outer surface.

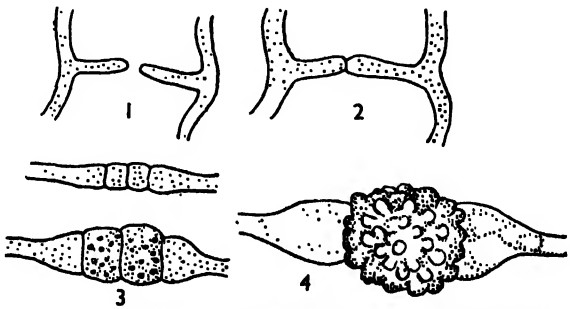


FIG. 68.—*Mucor mucedo* : stages in the formation of zygospore (after Heald).

MUCOR

The largest number of species in the Mucorales occur within this genus, and in its mycelial and reproductive characters it agrees completely with *Rhizopus* described above, except that the rhizoids and stolons are lacking. Sporangiophores are not fasciculate, as in *Rhizopus*, but arise singly from the mycelium. The life of heterothallic forms of *Mucors* is the same as that of *Rhizopus nigricans* but for the exceptions mentioned above (Fig. 68).

Even though plant parasitic forms are rare, a few of these black-moulds are reported to cause disease, especially fruit-rots. Much loss to young as well as mature apples is caused by *Rhizopus arrhizus* Fischer in Baluchistan. Some species of *Choanephora* occur on mature and faded flowers of *Hibiscus*, *Ipomoea* and *Zinnia*; and *Choanephora cucurbitarum* (Berk. & Rav.) Thaxter is parasitic on squashes and chillies.

KULKARNI, G. S., "Observations on the downy mildew, *Sclerospora graminicola* (Sacc.) Schroet. of bajri and jowar," *Mem. Dep. Agric. India, Bot. Ser.*, **5**, 268–274 (1913).
MIDDLETON, J. T., "The taxonomy, host-range and geographic distribution of the genus *Pythium*," *Mem. Torrey Bot. Cl.*, **20** (1), (1943).
MITTER, J. H., "Some recent contributions to our knowledge of heterothallism in fungi," *J. Indian Bot. Soc.*, **15**, 183–192 (1936).
STEVENS, F. L., "Gametogenesis and fertilization in *Albugo*," *Bot. Gaz.*, **32**, 77–98, 157–169, 238–261 (1901).
SUBRAMANIAM, L. S., "A *Pythium* disease of ginger, tobacco and papaya," *Mem. Dep. Agric. India, Bot. Ser.*, **10**, 181–194 (1920).
UPPAL, B. N., and DESAI, M. K., "Physiologic specialization in *Sclerospora graminicola* (Sacc.) Schroet," *Indian J. Agric. Sci.*, **2**, 667–678 (1932).
UPPAL, B. N., and DESAI, M. K., "Two new hosts of the downy mildew of *Sorghum* in Bombay," *Phytopath.*, **22**, 587–594 (1932).
UPPAL, B. N., and DESAI, M. K., "Koleroga disease of Areca nut," *Curr. Sci.*, **8**, 122–123 (1939).
WESTON, W. H., and UPPAL, B. N., "The basis for *Sclerospora sorghi* as a species," *Phytopath.*, **22**, 573 (1932).

CHAPTER VII

ASCOMYCETES

THE Ascomycetes or the sac-fungi are characterized by a well-developed thallus which is profusely branched. In the family Saccharomyceteae of the Endomycetales, however, mycelium is absent. The hyphae are regularly divided by septa into uninucleate cells; but multinucleate cells may also occur. The septa are actually incomplete transverse walls with a central perforation large enough to permit the streaming of cytoplasm from cell to cell.

Chlamydospores are common, and formed by the rounding of the terminal or intercalary mycelial cells. They are as a rule resting cells and contain reserve food substances. They germinate after a period of rest.

The imperfect forms reach the culmination of their development in this class. Gemmae, oidia and several kinds of conidia are known, and in some species several imperfect forms may appear successively or simultaneously. Conidia are borne on the conidiophores, which may be scattered or more often closely packed together in a subepidermal or subcortical layer. Conidiophores lie vertically in such layers, abutting on one another in a continuous manner. These layers are called **acervuli** if they are saucer-shaped (Fig. 13) and **sporodochia** if they are barrel- or sausage-shaped. Conidiophores may be enclosed in flask-like structures, the **pycnidia** (Fig. 15), in which case the conidia are known as **pycnidiospores**. Pycnidia are provided with openings at their apical end, known as **ostioles**.

Conidia are abstricted at the tips of the conidiophores, individually or successively. They may be formed in chains or they may be embedded in a mucilaginous drop. Conidial formation may be **acrogenous**, in which the basal conidium is the oldest and the one at the apex is the youngest; or it may be **basigenous**, in which the arrangement is reversed. Basigenous spore-formation is characteristic of *Erysiphe*. Conidia vary in shape, size and colour; if they are multicellular, they vary in the number and arrangement of cells. Their method of formation, arrangement and disposition on the conidiophores, and other morphological characters, are of much

importance in the determination of species. Conidia germinate without a rest period by putting forth germ-tubes and are usually viable for a short time.

Details of sexual reproduction in the Ascomycetes are known only in a few cases, and it is not possible to make generalizations. The mycelium is either homothallic or heterothallic, and the process of fertilization either isogamous or heterogamous. Copulation branches in the higher forms may undergo extensive functional and morphological differentiation, the male copulation branches becoming **antheridia** and the female **ascogonia**.

In the lower Ascomycetes—*Eremascus fertilis*, for example—sexual branches arise from neighbouring cells of the same hypha and grow side by side (Fig. 70). Each of them receives a nucleus from the parent cell, and finally one cell, considered the male, lies apposed to another, considered the female. After a time they fuse. The two nuclei also come together and fuse. The fusion nucleus enlarges, and the cell forms a spherical **ascus**. The fusion nucleus then divides three times, and eight ascospores are formed. The first division of the fusion nucleus is a reduction division.

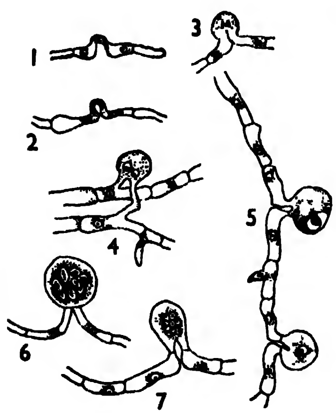


FIG. 70.—*Eremascus fertilis:* development of asci and ascospores (after Guillermond).

In the higher forms heterogamy is the rule and the antheridium is morphologically differentiated from the ascogonium. The ascogonium may consist of a single cell or more than one cell, and in some families it is characterized by the development of a receptive portion at the distal end, the **trichogyne**, which may be prolonged into a tubular structure (Fig. 71). The trichogyne may be septate or unseptate.

A union of the antheridium and the ascogonium results in the protoplasm of the former migrating into the latter. This may be through the lateral pore, or the trichogyne, if it is present. In *Pyronema confluens*, a homothallic species, the cells developing into antheridia become club-shaped and their nuclei divide and re-divide until there are one hundred or more. The ascogonium, as it matures,

produces a curved tubular trichogyne whose tip grows towards the upper end of the antheridium and curves again. A dissolution of the wall in the region of contact of the antheridium with the trichogyne takes place, and simultaneously a disintegration of the nuclei of the trichogyne and also its cross walls occurs. Several nuclei and most of the cytoplasm now pass into the ascogonium, and the male and female nuclei, which are haploid, become associated in pairs (Fig. 72).

This process marks the development of a new phase. The ascogonium, instead of forming an ascus immediately, as in lower Ascomycetes, gives rise to one or many, irregularly branched, tubular, outgrowths, known as **ascogenous hyphae**. Asci are eventually formed at their distal ends (Fig. 72). The ascogenous hyphae are the diploid generation of the plant, borne on the upper side of the ascogonium. They are not capable of forming independent mycelium, as they are dependent on the haplont mycelium for their nutrition. Young ascogenous hyphae are unseptate, but older ones have septa. They are surrounded by the haplont mycelium, and the resulting fruit body is made partly of haplont and partly of diplont mycelium. This fruit body is the **ascocarp**, and is very characteristic of the higher Ascomycetes. The ascocarp shows great variety in structure and organization. In some families its formation awaits the application of the fertilization stimulus, in others its development may reach an advanced stage before the sex organs are formed.

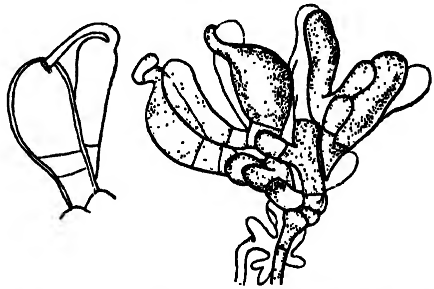


FIG. 71.—Fertilization in higher Ascomycetes; ascogonia and their trichogynes being fertilized by antheridia (after Kihlmann).

A fusion of the sex cells leads to an association, as already stated, of the respective male and female nuclei within the ascogonium. According to some cytologists the nuclei fuse in the ascogonium, and the ascogenous hyphae contain truly diploid nuclei. The fusion of the nuclei which again takes place within the ascus is, they state, a second fusion. If there are two fusions, the nucleus will have a four-fold number of chromosomes (tetraploids), and a double reduction division has therefore to take place. This, it is assumed, takes place in the first and third divisions in the ascus.

Several investigations have been carried out to clarify the position, and while opinions and interpretations are conflicting, the consensus of opinion favours the view that the male and female nuclei do not fuse in the ascogonium and that a single fusion in the ascus is the normal process, conforming in this respect to what happens in the Basidiomycetes. The nuclei become paired in the ascogonium, forming dikaryons, and pass as such into the ascogenous hyphae, and thus come to have a rather prolonged binucleate phase of development, with conjugate divisions of paired nuclei, terminated in the ascus by a nuclear fusion. The first division which takes place in the ascus

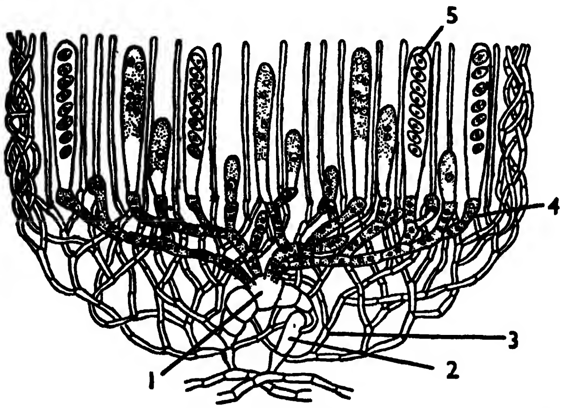


FIG. 72.—Diagrammatic view of fertilization in Peziza sp.: *1* ascogonium; *2* antheridium; *3* trichogyne; *4* ascogenous hyphae; *5* asci and ascospores (after Smith).

is a reduction division, and two successive mitotic divisions also follow, the chromosomes meanwhile returning to the haploid number.

The development of the ascogonium with its trichogyne into a complex structure is not paralleled by the antheridium, which shows no such complex structure. In fact it is possible to trace the gradual dwindling of its importance, ultimately leading to its elimination. With the gradual cessation of the function of the antheridium and the establishment of some sort of autogamic type of fertilization, the importance of the ascogonium itself is suppressed, and fertilization is ultimately effected between two undifferentiated cells of haploid mycelium. In *Lachnea stercorea* the antheridium and the trichogyne fuse, but no male nuclei pass into the ascogonium. In *Lachnea cretea* the antheridium is not formed, though the trichogyne is

present. In *Humaria granulata* the ascogonium retains its shape and forms the ascogenous hyphae, but the trichogyne has disappeared. Finally, in *Humaria rutilans* the ascogonium itself has disappeared, but a fusion of vegetative cells occurs. Although modification and even disappearance of the sexual organs takes place, the essential feature, which is a fusion of two haploid nuclei, is retained. It would appear that it is immaterial whether these nuclei are derived from sexual organs or from the ascogonium alone, or from an ascogonium and a vegetative cell, or from two vegetative cells. Parthenogenetic formation of asci occurs in the group.

Ascogonia are unicellular or transversely septate, and the ascogenous hyphae are either unbranched or profusely branched. In the latter case the branches intertwine with each other. They may be unseptate until later in their development, but most of them have transverse walls through all their stages of development. Their distal ends are binucleate and the ultimate binucleate branchlet terminates in a re-curved '**crozier-like**' cell which is also binucleate. The two nuclei in this cell divide simultaneously, and one pair lies in the arch of the crozier, known as the **arch cell** (Fig. 73). The arch cell enlarges and develops into an ascus. Early in the development of the ascus the male and the female nuclei fuse, and during their further enlargement divide in the manner stated above, usually forming 8, but sometimes 16, 32, 128, etc., nuclei. After the completion of the last series of nuclear divisions, the ascospores, which are as many in number as the nuclei that have ultimately formed in the ascus, are formed. They are cut by free cell formation, leaving in the ascus a certain amount of unused cytoplasm, known as '**epiplasm**'. This contains glycogen and other food substances which supply nutrition to the developing spores. The asci may be spherical, oval, club-shaped or almost cylindrical, with a more or less elongate base. The arrangement of the spores within the ascus is important, as it is constant for the species. Ascospores may be arranged in uniseriate, biseriate, fasciculate or in inordinate manner. For their release the ascus opens explosively, either by means of a tear or by dehiscence, along a definite line, and

FIG. 73.—Crozier formation.

the spores may be shot out in a jet of liquid. These explosions may be simultaneous or successive. In a few cases the asci are provided with a lid-like structure for the ejection of the spores, the **operculum.**

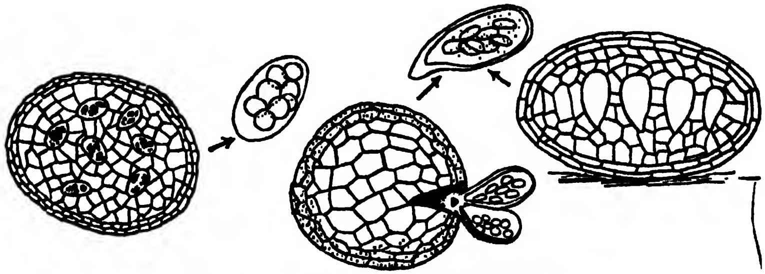


FIG. 74.—Cleistothecia of *Erysiphe* sp.

The ascocarp is of three kinds, the **apothecium** (Fig. 75, *2*) the **perithecium** (Fig. 75, *1*) and the **cleistothecium** (Fig. 74). The apothecium is an ascocarp in which the hymenium lies exposed while the asci are maturing. It has the shape of a saucer or an inverted bell. Within the hymenium are slender hairs about the

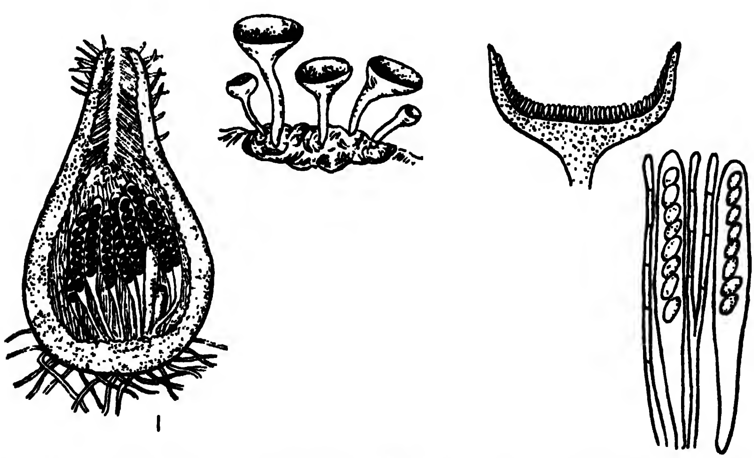


FIG. 75.—*1* Perithecium of *Podospora fimiseda* (after von Tavel); *2* apothecia of *Sclerotinia* (after Heald); asci and ascospores.

same length as the asci but developing a little earlier. They have no connection with the ascogenous hyphae, are haplont in character, and are known as **paraphyses.** They have a protective, and possibly a distributive, rôle. They are placed perpendicularly to the surface of the hymenium and terminate at a uniform height.

Perithecia are round or flask-shaped ascocarps. An outside wall, known as a **peridium**, encloses the hymenium. A narrow aperture, the **ostiole**, is also present at the apex, for the discharge of the ascospores. The asci are inside the perithecium on the side opposite the ostiole and are borne on the ascogenous hyphae. They may also be spread over the inner surface of the wall and converge radially towards the centre.

The cleistothecium is a perithecium without an ostiole. Asci in a cleistothecium may be arranged in a hymenial layer or irregularly placed at different levels.

The Ascomycetes are divided into two sub-classes as follows:

Asci formed singly, directly from the zygote, sometimes closely aggregated, but no ascocarp formed	**Hemiascomycetes**
Asci formed directly from a zygote from which more than one ascus are formed and asci borne in ascocarps	**Euascomycetes**

The Hemiascomycetes are divided into two orders, and the Euascomycetes into fourteen orders, of which the following genera are phytopathologically, or otherwise, important: *Saccharomyces*, *Protomyces*, *Taphrina*, *Aspergillus*, *Penicillium*, *Erysiphe*, *Uncinula*, *Claviceps*, *Ceratostomella* and *Sclerotinia*. Diseases caused by some of their species are dealt with below.

SACCHAROMYCETACEAE

The fungi belonging to this family are known as yeasts which are used in making bread, because of their ability to lighten the loaf by filling it with bubbles of carbon dioxide, and in the production of alcohol by the fermentation of sugar. They have the ability to synthesize B vitamins, of which they are the richest source. They permanently maintain a unicellular form of growth, the cell being spherical, ovoid, ellipsoid and occasionally much elongated. The cells occur in masses, sometimes in chains or filaments. The cell-wall is relatively thin in young yeasts, but may occasionally be thickened in the old. Young cells have a relatively homogeneous protoplasm and a large nucleus, but vacuoles appear as they increase in size (Fig. 76, *1*). In older cells the cytoplasm and the nucleus constitute a relatively small portion of the cell contents.

Most of the common yeasts multiply by budding. In such cases

a minute protuberance on one side of the cell first becomes manifest and, by the division of the nucleus, is provided with a daughter nucleus. The protuberance rapidly increases in size and gets separated from the mother cell (Fig. 76, *1*). Sexual reproduction takes place and results in the formation of asci and ascospores (Fig. 76, *2*).

Saccharomyces cerevisiae Hansen exists both in haplophase and diplophase. Haploid cultures are more variable than diploid. Haploid cells tend to grow in clusters because of the failure of full-sized daughter cells to separate, and settle down to the bottom of the vessels. Haploid cells have a single set of genes, which are the ultimate source of substances which distinguish one living form from another. Diploid cells have greater stability in cell-size and shape, and produce uniform, large, smooth colonies. Two complete sets of genes occur in diplont yeasts. Haplophase cells, when paired, copulate to produce diploid cells, provided the haplophase cultures are of complementary mating types—that is, they are male and female strains. Copulation tubes, zygotes and asci are produced, the latter containing four haploid ascospores. If the ascospores are designated *A*, *B*, *C* and *D*, and then grown separately, they will give rise to only haplont cells. If they are mated, copulation takes place only when the cells of complementary mating types are brought together. It has been found that two ascospores, say *A* and *D*, belong to one mating type, and two others, say *B* and *C*, to the complementary mating type. When *A* and *B*, *A* and *C*, *C* and *D* or *B* and *D*, are paired, then mating takes place, but not otherwise.

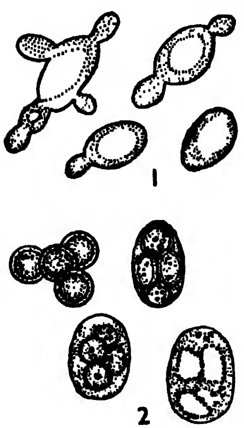


FIG. 76.—Yeast, *Saccharomyces cerevisiae* : *1* budding of cells; *2* formation of asci (after Guillermond).

Among yeasts *Saccharomyces cerevisiae* is the best-known species, being the common brewer's and baker's yeast. It has been intensely studied, and is perhaps one of the few plants cultivated under factory production methods. *Saccharomyces ellipsoideus* is found on grapes in nature and is extensively used in wine-making. *Torulopsis utilis* can synthesize protein from carbohydrates and inorganic sources of nitrogen. This is a very palatable yeast, and the protein

it contains is of high biological value and is an excellent source of B group vitamins.

PROTOMYCETACEAE

There is a single genus, *Protomyces*, in this family whose species parasitize higher plants, causing galls and tumours. They have an intercellular, irregularly branched, and septate mycelium. Reproduction is by means of chlamydospores which are subepidermal or distributed at various depths in the host tissue. They are multinucleate with a more or less thick and smooth membrane. They are intercalary or terminal and germinate only after a long rest period. The chlamydospores lying deep in the tissues germinate without breaking the exospore, but those nearer the surface of the host plant burst the exospore, and the contents bulge out into a vesicle covered by the inner wall.

The position of the family Protomycetaceae has long been a subject of speculation. Some mycologists consider the fructification to be a sporangium, and the family is doubtfully placed by them in the Phycomycetes near the Chytridiales. The spores are considered as zoospores, the motility of which has become lost. Others consider the fructification to be a chlamydospore, and the family is then doubtfully placed in the Ascomycetes, with which, however, it does not show any relationship. Only a single species, *Protomyces macrosporus* Unger, occurs in India, which causes a disease of coriander plants.

Stem-Galls of Coriander (*Coriandrum sativum* L.)

This disease of coriander caused by *Protomyces macrosporus* Unger appears in the form of tumour-like swellings on the veins, leaf-stalks, peduncles and other green parts of the plant (Fig. 77, *1*, *2*). The swellings are about an eighth of an inch broad and up to half an inch long. The fungus is restricted to the tumours, where broad, irregularly branched, closely septate and intercellular mycelium is found. After a time, single cells, which are the chlamydospore-initials, swell here and there in the mycelium, forming ellipsoid or globose bodies, and these are later developed into chlamydospores (Fig. 77, *3*). As they mature, they are surrounded by a thick, hyaline, three-layered wall, attaining a diameter of 50–60 μ. They are the resting bodies and are formed in large numbers. After a period of time, the chlamydospores germinate if immersed in water. The exospore

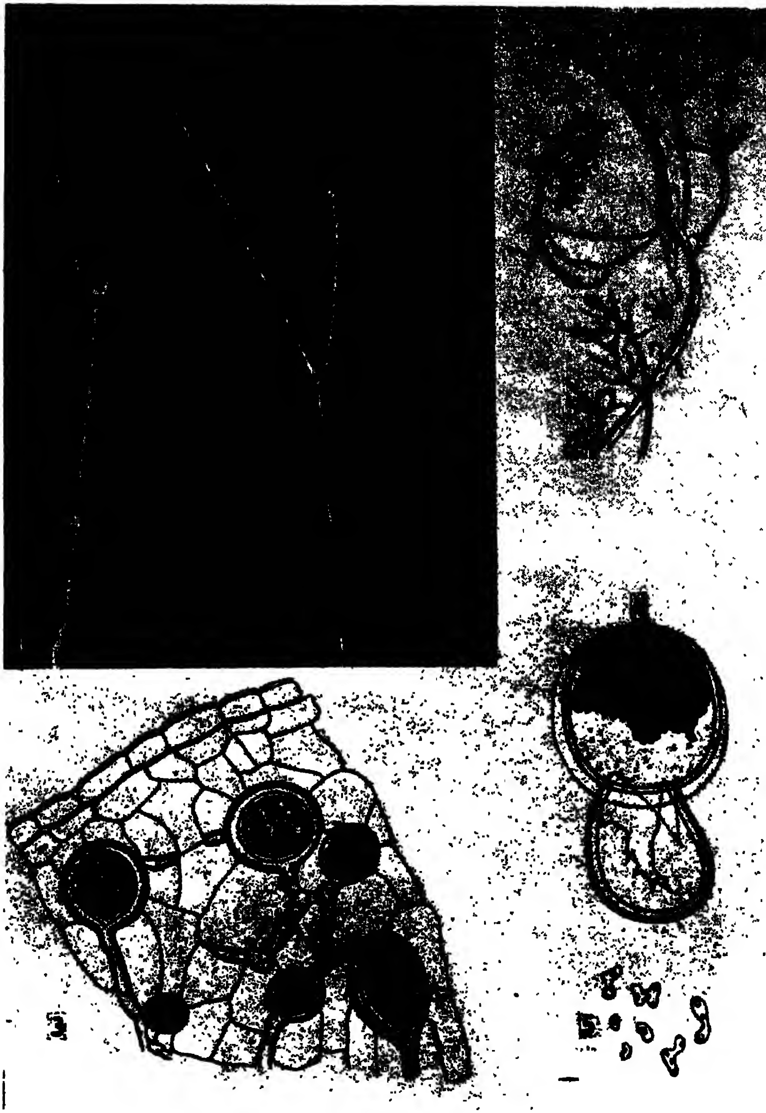


FIG. 77.—*Protomyces macrosporus*: *1* and *2* affected stems and inflorescence; *3* mycelium and chlamydospores in host tissue (after Butler); *4* germination of chlamydospore and first stage in spore-formation; *5* spores, some uniting in pairs (*4* and *5* after de Bary).

ruptures, and the inner wall is pushed into a vesicle or balloon, which remains at the mouth of the crack (Fig. 77, *4*). The protoplasm in the spore flows out into the vesicle, where it is gathered in a single peripheral layer, leaving the centre empty except for cell-sap. The nucleus divides several times, resulting in 100–200 daughter nuclei. These migrate to the periphery, and very soon cleavage planes start from the outside of the peripheral layer, and the protoplasm is divided into several uninucleate masses. These masses divide again and again, forming four ellipsoidal spores out of each mass. When fully mature, the spores separate from each other and collect out at the centre of the vesicle. The latter then bursts and the spores are set free. If conditions for resuming the parasitic life are lacking, these spores continue to multiply vegetatively by budding, like yeast cells. When a suitable host is available, they infect it. Penetration by spores into the host is not through the stomata, but by direct entry of the germ-tubes through the cell-wall into the epidermal cell.

The disease is widespread, and does more harm than was once thought. In cases of severe attack, seed may not be formed at all, but the disease has not been fully investigated, and remedial measures are unknown.

TAPHRINACEAE

The fungi belonging to this family, of which *Taphrina* is the most representative genus, are true endoparasites, strictly confined to definite hosts. They have a more or less richly developed septate and hyaline mycelium which grows intercellularly below the epidermis or in the deep-lying tissues of the host. In many species, perennating mycelium has been found.

There is no definite ascocarp, but a thin hymenial layer occurs on the surface of the host. It is not clearly defined or delimited and consists of asci, without paraphyses, standing in a palisade-like manner. The asci arise by the transformation of ascogenous cells, which are at first binucleate; but as the ascus matures, the two nuclei fuse, forming a large diploid nucleus. The binucleate condition found in the ascogenous hyphae extends back into the vegetative hyphae, where each cell exhibits one or more pairs of nuclei. When and where this binucleate condition arises has remained an open question. In certain species—for example *Taphrina epiphylla* —the ascospores are uninucleate and haploid, but in nutrient solu-

tions produce sprout conidia which are also uninucleate. The sprout conidia of the third and subsequent generations copulate, the nucleus of the one conidium passing into the other without nuclear fusion taking place. The dikaryotic phase continues for some time, the nuclei dividing conjugately. Karyogamy occurs just prior to the formation of the ascus, and this is followed by meiosis. Two more divisions take place, resulting in the formation of eight nuclei and then a like number of ascospores. In *Taphrina deformans* the nuclear cycle seems to differ, as copulation prior to infection of the host has not been observed. The binucleate condition is brought about by the conjugate division of the haploid nuclei of the spore at the time of infection, resulting in a pair of nuclei,

Individual asci are cylindrical, thin-walled, hyaline or with bright contents. Each ascus contains eight ascospores, which are one-celled, almost globose, thin-walled, hyaline or bright yellow. The pathological effects produced by these fungi are of various kinds. The leaves curl (Fig. 79), with hypertrophy and hyperplasia in the affected parts, causing 'witches' brooms'. Sometimes there may be only spotting, the spots resembling the pustules caused by rusts. In the latter case curling and twisting of leaves does not take place.

Leaf-Spot of Turmeric (*Curcuma longa* L.)

A leaf-spot of turmeric due to *Taphrina maculans* Butler is common in several parts of India. In turmeric-growing areas of Gujerat and Northern Circars (Madras) it causes considerable damage, and reports of the appearance of the disease in an epidemic form have been received from Orissa and Hyderabad (Deccan). A few other species of *Curcuma* and some of *Zingiber* are also attacked by the same fungus.

Attacked plants are not killed, but owing to excessive spotting and destruction of the assimilative and chlorophyll-bearing tissues of the leaves, heavy reduction in yields occurs. The spots appear in great numbers (Fig. 78, *1*), thickly covering both sides of the leaf-surface, and the attacked leaves bear a reddish-brown appearance, instead of the normal green. There is etiolation, the leaves becoming yellow much sooner than they normally should. The spots are small, usually one to two millimetres in diameter. Discoloration ultimately becomes badly defined, but there is no distortion of the leaves (Fig. 78, *1*).

The mycelium is between the cuticle and the epidermis, and the

hyphae send branched or lobed haustoria into the host tissues. The hyphae are confined to the epidermis, and may continue down in the vertical walls of the next layer of cells, but do not penetrate farther, except to send an occasional haustorium into the spongy parenchyma. When the spots are fully developed, their central portions are occupied by an almost continuous layer of hyphae. The outer cells of this layer grow into cylindrical or club-shaped, thin-walled projections

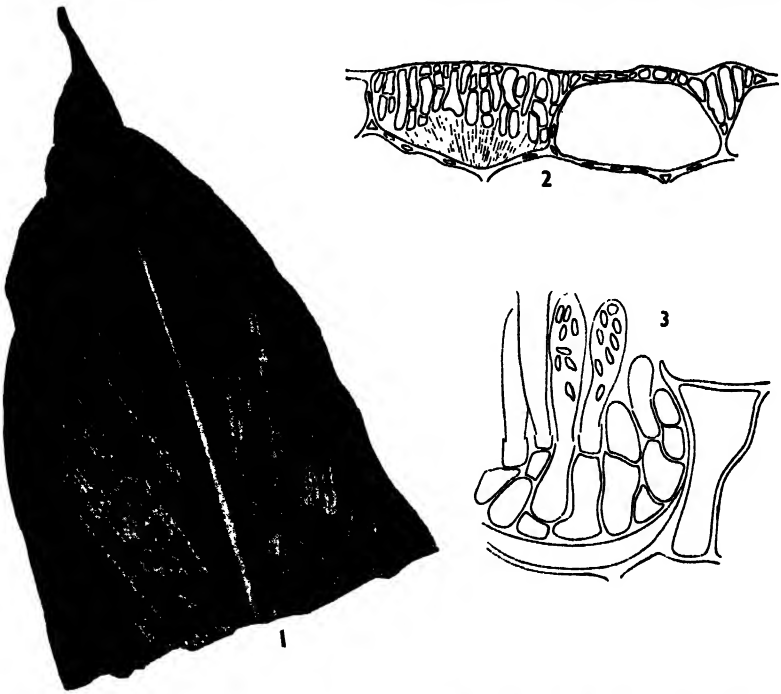


FIG. 78.—Leaf-spot of turmeric: *1* part of leaf with spots; *2* mycelium; *3* asci and ascospores of *Taphrina maculans* (after Butler).

which rupture the epidermis and become asci. Asci are found on both sides of the leaves. All of the outer cells of the fungus are ascogenous, but they mature at different intervals, so that ripe asci are found in little groups. There is one basal cell below the ascus, but more may occur. The asci measure 20–30 by 6–10 μ, and usually contain eight ascospores which are ovoid, hyaline, unicellular, and measure 4–7 by 2–3 μ. They multiply by budding which may start even within the ascus itself. The fungus has recently been grown in culture media.

The precise mode of transmission of the fungus is as yet unknown, and how long the ascospores remain viable in plant debris has not yet been ascertained. It is unlikely that the mycelium reaches the rhizomes to remain there in a dormant state and then give rise to the disease when the seed-pieces are sown the following season. It is possible that dried leaves bearing the spots and lying about in the fields with their asci are the chief source of the subsequent year's infection. If the precise time of appearance of the disease, relative to the age of the plants, is known, and if the relation between the phenological conditions and the incidence of disease is also determined, then it should be possible to protect the plants with a suitable spray or dust, so that both the upper and the lower sides of the leaves are fully covered to prevent infection. Bordeaux mixture or any one of the recently developed non-metallic fungicides is likely to control the disease effectively.

Leaf-Curl of Peaches (*Prunus persica* Stokes)

Leaf-curl of peaches caused by *Taphrina deformans* (Berk.) Tulasne is prevalent in the peach orchards in Kumaon, Kulu, and other parts of the sub-Himalayan range and in the peach-growing sections of the North-West Frontier Province. The disease is often very severe, and the affected trees stand out conspicuously with their distorted and discoloured leaves. The disease first becomes manifest in early spring, when the leaves of the affected trees become thickened, puckered, curled downwards, and often greatly distorted. As a rule the entire leaf is affected, but in some leaves only a part may show blistering. At first the attacked leaves are pale green or yellowish, but later they become reddish, thick, and more fleshy than the normal leaves. After a time the upper surface is covered with a whitish bloom as the fungus begins to produce its spores. The leaves are finally killed and shed, resulting in severe defoliation. The trees lose their vigour, and the crop suffers in quality and quantity (Fig. 79).

Young shoots attacked by the fungus become swollen and distorted, and even the flowers and fruit may be affected. It was at one time believed that the fungus hibernated in the shoots in the form of dormant mycelium and produced infection in the following year. Recently it has been shown that the primary attack is due solely to ascospores and sprout conidia that persist through the winter on twigs, buds and scales. They are washed down by the spring rains

and are lodged on the unfolding leaf-buds. In early spring, when the temperatures are cool and the weather is wet, the spores germinate and attack the tender tissues of the host plant. The intensity of infection is therefore largely influenced by the weather conditions that are present at the time the tree comes into leaf.

The mycelium is intercellular and grows in the tissues, obtaining

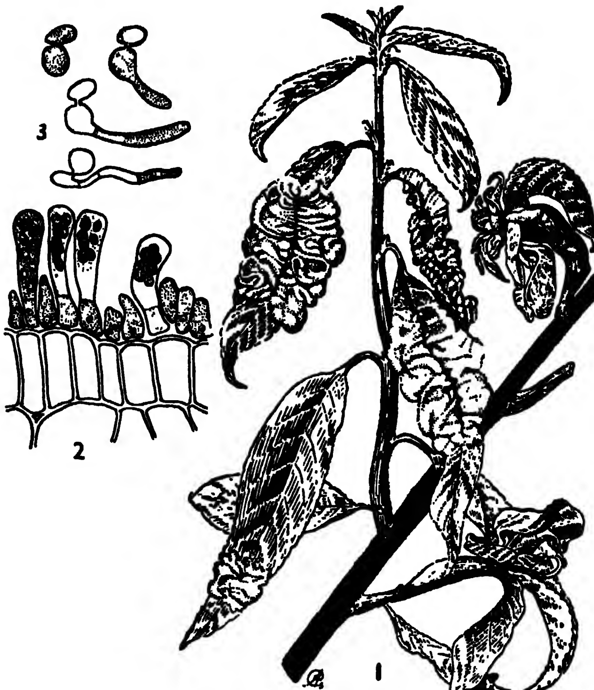


FIG. 79.—Leaf-curl of peaches due to *Taphrina deformans*: *1* branch showing attack; *2* asci and ascospores; *3* fusion and germination of ascospores (after N. B. Pierce).

its nutrition from the host. The host reacts by putting forth increased growth, which, however, does not take place evenly, but only towards the upper surface of the leaves, causing puckering and downward-curling. A layer of hyphae develops about this time beneath the cuticle, and numerous cylindrical cells grow up from it, rupturing the epidermis. These cells are mainly ascogenous cells which later develop into asci. Each ascus contains eight ascospores, but these may bud and give rise to secondary spores, known as

sprout conidia. The asci and the sprout conidia can withstand desiccation and remain viable for long periods.

On germination the ascospores form infection threads which fasten themselves to the leaf-surface. The infection threads press against the thick cuticle, and the fungus slowly grows within it. Intracuticular growth takes place only for a short time, for the fungus soon begins to grow into the leaf-tissues, forcing its way between the epidermal cells until it reaches the less compact parenchymatic tissues beneath the epidermis.

The fungus over-winters in the form of ascospores and sprout conidia, which are lodged on the surface of the trees, but do not cause infection until the following spring. If they are washed down at that time and lodge on the young unfolding leaves and buds, they infect the young meristematic tissues. Mature tissues are not attacked by the fungus. Carefully timed sprayings with Bordeaux mixture adequately control leaf-curl, provided they are applied very thoroughly. One such spraying in autumn and another in spring, just before the buds open, are stated to reduce the disease considerably in Canada.

ASPERGILLACEAE

Species belonging to this family are the common moulds found on all organic matter. They are as a rule saprophytes, but a few are animal parasites causing diseases known as **mycoses.** Many species of *Aspergillus* and *Penicillium* are responsible for rots and decays of fruit inside which they gain entrance through wounds or bruises and cause pulp-rots and other decays. The importance of the species of this family is chiefly due to their use in industrial processes, especially the production of citric acid, gluconic acid, glycerol and drugs like penicillin and flavicin, and in the ripening of cheese.

In *Aspergillus* the mycelium is hyaline, bright or pale-coloured, and bears on its surface concretions of colouring matter, but it is not, by itself, black or smoky brown. In *Penicillium*, too, it is hyaline, pale or brightly coloured, but in both the genera it is partly submerged in the substratum and partly aerial. In *Aspergillus* the conidiophores arise from specially differentiated "foot" cells (Fig. 80), but in *Penicillium* they arise from undifferentiated mycelial cells. They are mostly unseptate in *Aspergillus*, but septate in *Penicillium* (Fig. 81). The conidiophores in the former enlarge towards the apex into a vesicle on which the conidia-bearing cells,

the **sterigmata**, are produced simultaneously. Conidia are either borne directly on these sterigmata or the sterigmata may branch and form secondary sterigmata on which the conidia are borne. In

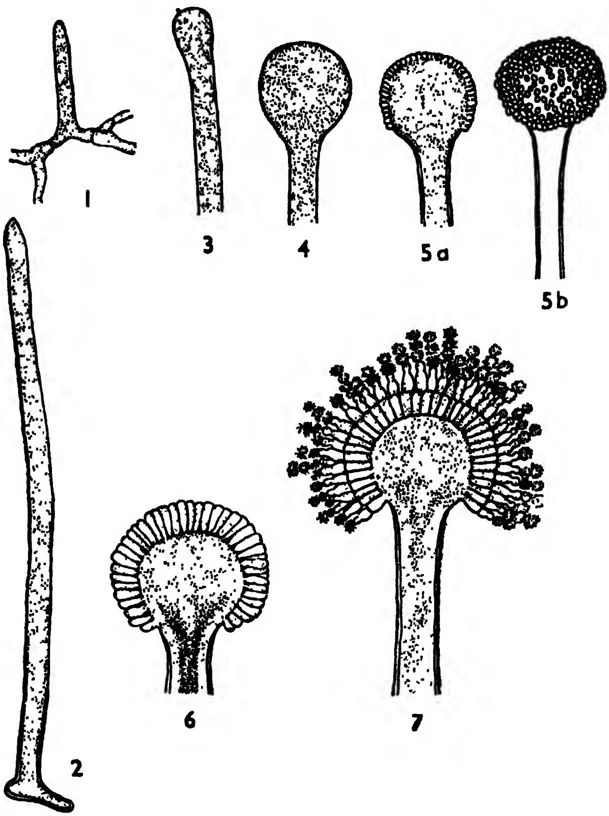


FIG. 80.—*1* Foot cell bearing young conidiophore; *2* developing conidiophore; *3* and *4* development of the vesicle; *5a* and *5b* vesicle in optical section and surface view showing development of sterigmata; *6* later stage in development of sterigmata; *7* young fruiting head showing secondary sterigmata bearing chains of conidia. × 265 (after Thom and Raper).

Penicillium the conidiophores may be aggregated into fascicles or compacted into coremia, ultimately terminating in a broom-like whorl of branches, the **penicillus**. The penicillus consists of a single whorl of sterigmata or it may be twice or thrice branched, the final branches bearing the conidia, being produced by abscission.

Conidia are produced in chains and are smoky or black in *Aspergillus*, but green in *Penicillium*.

Ascocarps occur in both the genera. They are without an ostiole, and are in fact cleistothecia. The development of asci varies from species to species, and no generalizations can be made. In *Penicillium vermiculatum*, which is heterothallic, the ascogonium when young is uninucleate, but it divides and re-divides to form thirty-two

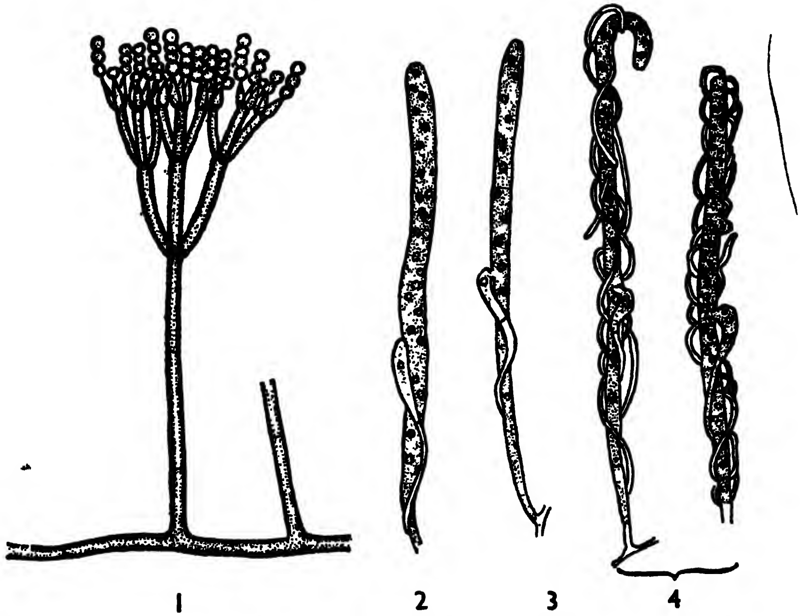


FIG. 81.—*Penicillium vermiculatum* : *1* conidiophore, sterigmata (phialides) and conidia; *2* multinucleate ascogonium and young antheridium; *3* fusion of antheridium and ascogonium; *4* ascogonium surrounded by sterile hyphae and divided into binucleate cells which are beginning to develop ascogenous hyphae (*2*, *3* and *4* after Dangeard).

or sixty-four daughter nuclei. The antheridium is also a uninucleate branch which spirals round the elongate ascogonium and eventually forms a short, somewhat inflated, uninucleated antheridial cell at its distal end. The tip of the antheridial cell comes into contact with the ascogonium, a dissolution of the cell-walls takes place, and a gametic union of the antheridial and ascogonial protoplast and nuclei is brought about. Sterile hyphae now grow around the united antheridium and ascogonium and develop into the peridium of the ascocarp. Later ascogenous hyphae arise and

mature asci lie irregularly distributed in the ascocarp. In *Aspergillus* the asci and ascospores are globose and bright red or yellow.

ERYSIPHALES

Erysiphales are characterized by their obligate parasitism and by being typically ecto-parasitic. The ascocarp is a more or less globose cleistothecium with a compact pseudo-parenchymatic peridium. The asci occur as a layer of parallel structures at the base of the cleistothecium, but forms where the entire cleistothecium consists of a single large ascus are known.

Many species have been cytologically investigated because of their abundance, simple structure and possession of typical ascigerous and conidial stages. The mycelium is entirely superficial except in *Leveillula*, and its conidial stage *Oidiopsis*, where it is endophytic. It is hyaline, branched and septate, and its cells are uninucleate. It fastens itself to the host by means of appressoria and penetrates the epidermal cells by means of uninucleate haustoria which have a characteristic lobed appearance.

Asexual reproduction is by means of conidia which are borne on the conidiophores. The latter are simple, short, erect, and as a rule unicellular. Conidia arise in basipetal succession and are hyaline, barrel-shaped, smooth and one-celled. They germinate readily in humid air, producing one to three germ-tubes. They form appressoria if a contact stimulus is applied. They are summer spores and short-lived.

Ascocarps are sub-spherical, often somewhat flattened, white to yellow when young, dark brown to black and reticulated when mature. They are provided with appendages of various types, which are of much importance in distinguishing genera. Asci are either solitary or numerous and bear two to eight ascospores.

Powdery Mildew of Peas (*Pisum sativum* L.)

The powdery mildew of peas, due to *Erysiphe polygoni* DC., appears in an epidemic form almost every year when the plants are in pod stage towards the end of January and in February. Unlike the downy mildew which is favoured by moist weather, this mildew is easily the worst disease of peas when conditions are dry. Several other leguminous crops are attacked by this fungus, and the disease is widely distributed all over the world.

The earliest symptoms of the disease appear on the upper surface

of the older leaves as small, white, circular, powdery spots. These spots enlarge rapidly, cover the entire upper surface, and later the lower surface may also become infected. On the midribs and the veins, the spots are first circular, but later become elongate. The fungus grows rapidly over the surface of the leaves, and in advanced stages the foliage appears as though it is covered by a talcum-like powder. The leaves may become reduced in size, turn yellow, and are finally shed. Immature pods are also attacked, getting shrivelled and dried. On such pods, however, there are no distinct and properly defined spots, but the fungus appears as a powdery coating over the entire surface.

The mycelium consists of delicate and persistent hyphae which are attached to the leaves by means of appressoria. Haustoria arise as narrow tubes from the appressoria, penetrate the epidermis and swell into lobed and round sacs in the epidermal cell. Conidiophores arise vertically from the leaf-surface and bear several spores which are in chains. They are formed in regular order from the top backwards, and ripe spores are wafted by wind. Spores are copiously produced and give the leaves a characteristic appearance. They are elliptical, barrel-shaped, or sometimes even cylindrical. They are 35–45 μ in length, 15–19 μ in breadth, and hyaline. Later in the season ascocarps appear as sharp, black specks scattered on the surface of the white mycelium. The ascocarps (Fig. 82) are globose, up to 90 μ in diameter, and composed of distinctly polygonal cells. They are covered by hyaline to dark, free or interwoven, appendages. A limited number of asci, from two to eight, are formed within the ascocarps. The asci are ovate, almost sessile, 46–72 μ in diameter, with four to five ascospores in each ascus (Fig. 82, *2*). The ascospores are elliptical, one-celled, hyaline, and measure 19–25 μ in length and 9–14 μ in breadth.

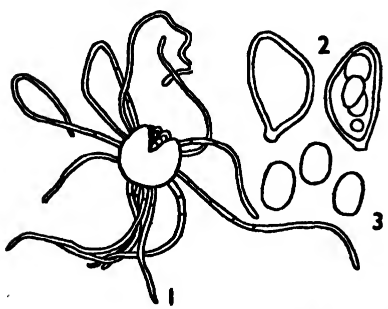


FIG. 82.—Powdery mildew of peas, *Erysiphe polygoni* : *1* cleistothecium with appendages; *2* asci and ascospores (after Peterson).

Primary infection in the field is stated to be due to the dormant mycelium in the pea seeds, and experiments conducted at Poona have

indicated that if such seed is treated with water at 50° C. for ten minutes, the disease can be controlled to some extent. The ascocarps that persist in the soil or plant debris may form another source of primary infection. Dusting the plants with sulphur at the rate of 25 lb. per acre gives perfect control. Sulphur dust for this purpose must be of extreme fineness, capable of passing through a sieve with at least 200 meshes per linear inch. The precise dates when the mildew usually appears must be correctly determined, as far as possible, and the dusting operation must be done a day or two before that date. As a rule a single dusting gives complete control.

Erysiphe polygoni has been shown to consist of specialized races, each restricted to a particular host or group of related hosts. The form on garden peas (*Pisum sativum*) can attack field peas (*Pisum arvense*) but presumably not other hosts.

Powdery Mildew of Barley (*Hordeum vulgare* L.)

Powdery mildew of cereals is not of much importance in the plains of India, excepting in the sub-montane districts of the north. When favourable environmental conditions permit widespread infection, it has been especially noticed on barley, particularly in the United Provinces and Bihar.

The fungus, *Erysiphe graminis* DC. var. *hordei* Marchal, is generally limited to the leaves the upper surface of which is more severely affected than the lower. When conditions are suitable, the sheaths, stems and glumes may also be affected. The fungus forms numerous colonies of superficial, flocculent growth, first as small felty masses of mycelium and conidia. They are white to begin with, then grey or reddish. The colonies have a powdery appearance and form a cushion-like growth. As a result of mildew, the leaves transpire more profusely than the normal leaves. Infected plants become stunted through a reduction in the size and number of leaves. Leaves that are not shed become crinkled, spirally twisted and deformed.

The mycelium is superficial, sparingly branched, with small flat appressoria and haustoria. Haustoria penetrate the epidermal cells, where they produce characteristic finger-like projections extending into the host cells (Fig. 83). Conidiophores arise from the superficial mycelium at right angles to the leaf-surface. Conidiophores are swollen at the base in a characteristic manner. The cylindrical outgrowth above the basal cell divides into two cells, each of which again

divides, developing later into barrel-shaped conidia. New conidia are produced by the elongation of the basal cell in its upper part, and this is continued until ten to twelve conidia are produced (Fig. 83). Conidia ripen from the apex downwards. When mature they are elliptical, hyaline, one-celled, and measure up to 30 μ in length and 10 μ in breadth. They germinate by the production of several germ-tubes. Cleistothecia, which are rarely produced in India, are up to 200 μ in diameter, globose, black, and partly immersed in the

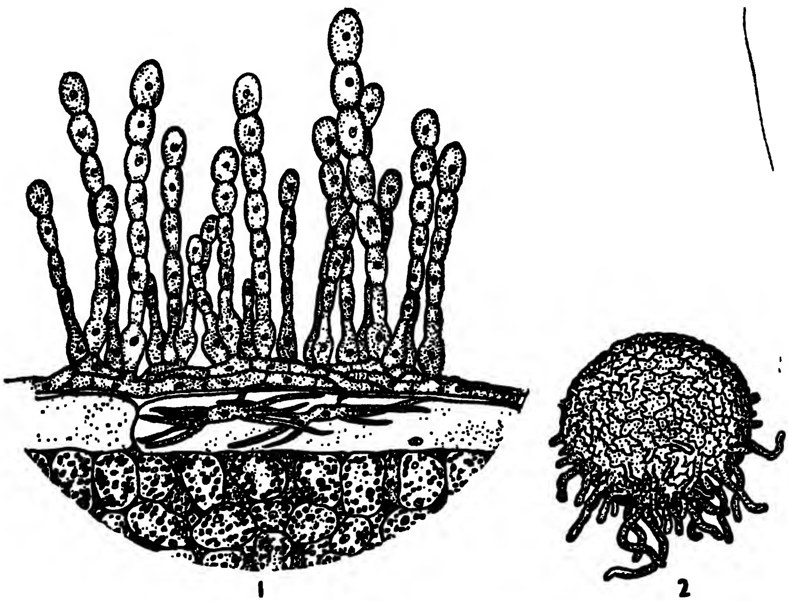


FIG. 83.—Powdery mildew of barley: *1* conidiophores, conidia and haustoria of *Erysiphe graminis*; *2* a cleistothecium of the same fungus (after Melhus and Kent).

mycelium. They are provided with simple or slightly branched appendages. In each cleistothecium there may be as many as twenty-five asci, each with four to eight elliptical ascospores.

Conidial germination is highest at 12° C., while the best growth of the germ-tubes is at 21° C. They germinate better on dry slides in moist air than when they are placed on or in drops of water.

Erysiphe graminis consists of specialized races which are quite sharply restricted to certain hosts. There appear to be, so far as at present known, seven varieties of the fungus, each variety being

further segregated into several races. It is claimed that six races are known on barley alone.

Direct control by the use of sulphur dust is possible, but the cost of treatment is prohibitive, and there is little likelihood of its being adopted. There may be differences in the reaction of different varieties of barley to this mildew, but little work has so far been done to exploit this possibility of controlling the disease in India.

Powdery Mildew of Grapes (*Vitis vinifera* L.)

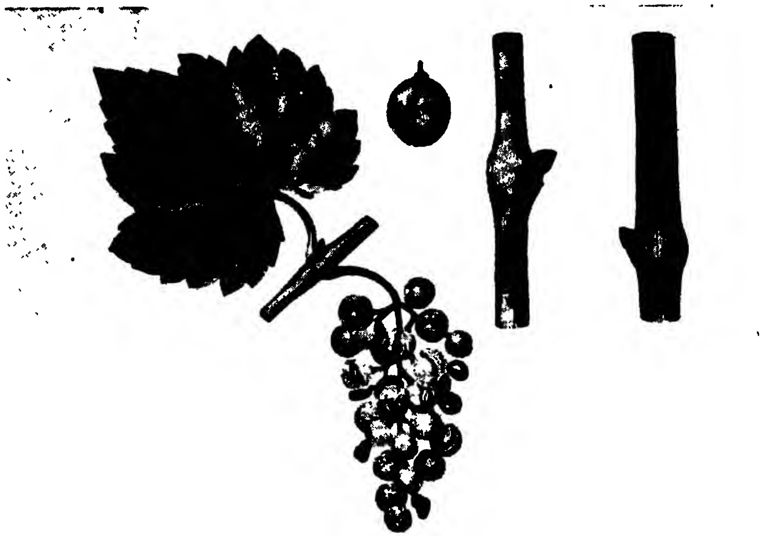
The powdery mildew of vines is a common disease all over the Old and New World, and when conditions are favourable it appears in an epidemic form wherever the crop is grown in India. It is caused by *Uncinula necator* (Schw.) Burrill, the leaves, stems, flowers and fruit being attacked (Fig. 84). In young leaves small whitish patches appear on the upper or lower surface, and as the disease progresses these patches run together, until a large part of the surface of the leaves is covered with a whitish-grey mildew. Malformation and discoloration of the affected leaves are common symptoms. Diseased vines have a wilted and dwarfed appearance. Affected stems have a greyish tint, and if the attack is not severe mildew appears in patches. Later the stems turn dark brown. Blossoms and berries are also attacked. If the attacked berries are half grown or nearly mature, they become irregular in form and only a very few ripen; those that do so are much reduced in size and quality, and develop cracks. If the attack is quite early, the berries rarely develop and are shed.

The whitish colour of the mildew is due to the mycelium and the conidiophores. The mycelium is attached to the leaf-surface by means of appressoria, from which haustoria are sent into the epidermal cells of the host to obtain their nutrition. Conidiophores arise from the mycelium and are simple and erect. Conidia are produced in chains in a basigenous manner, each conidiophore thus producing a large number. Conidia are egg-shaped, light, and easily disseminated by wind (Fig. 84, *3*).

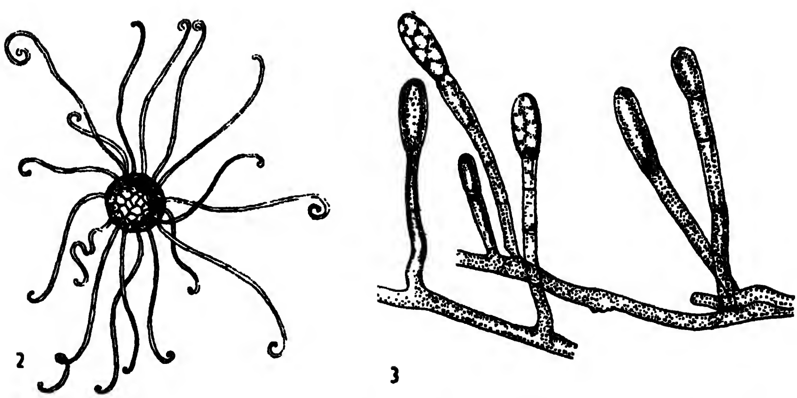
The perfect state is not formed under conditions obtaining in the plains of India, but abundant formation of cleistothecia has been noted in Baluchistan. The cleistothecia (Fig. 84, *2*) are almost spherical, and contain from four to eight asci. Each ascus contains from four to six ascospores. Appendages, which are septate and coiled at the free end, occur on the ascocarps.

At Nasik (Bombay), where there is extensive grape cultivation, it

een noted that climatic conditions in October and November, temperatures are between 28° and 35° C., are ideal for the



1



2

3

FIG. 84.—Powdery mildew of grape, *Uncinula necator* : *1* affected leaves, fruit and stems; *2* cleistothecium of same; *3* conidiophores and conidia (*2* and *3* after Rostrup).

development of the mildew. Warm, dry weather with just enough humidity is very favourable. As bright sunlight retards the growth of the fungus, cloudiness helps the disease.

Dusting the vines with sulphur dust that passes through a sieve with three hundred meshes per linear inch gives effective control. The first application, it has been found, should be made when the new shoots are 3–6 inches long, and the second during or just before blossoming. Forty to fifty days later a third application is given, and the fourth, which may not always be necessary, fifteen to twenty days after the third. Sulphur does not scald or stain the berries, and if the dusting operation is done in time the control is quite complete.

SPHAERIALES

The order Sphaeriales, consisting of fifteen families and over a thousand species, is the most characteristic of the class Ascomycetes. The mycelium is hyaline and freely branched, and asexual reproduction has reached its highest degree of development in the order. The types of conidial production are most varied, and as perithecial formation is rare, conidia serve to perpetuate the species. Conidia may be produced on free conidiophores or conidiophores held together in an acervulus or enclosed within a pycnidium. A majority of the Fungi Imperfecti are the conidial stages of this order, some forming their perfect states in culture media when the conditions necessary for their formation are present. It is possible that in many cases several species have permanently lost their power of sexual reproduction.

Perithecia are variously modified and the perithecial wall is generally dark-coloured, more or less hard or carbonaceous, and free from the enclosed asci, which arise from the base or part-way up the base of the perithecium. Asci form a dense hymenium or they may be more loosely arranged. Delicate and evanescent paraphyses are present, but **periphyses** (i.e., paraphyses-like threads at the edge of the hymenium but not intermingled with the asci) are more frequent. The asci, which are generally clavate, do not have an operculum. The ascospores may be expelled through a pore at the apex of the ascus or by rupturing of the ascus-wall, or the upper half of the ascus may break. Ascospores lie in one (uniseriate), two (biseriate) or many (multiseriate) rows, or in a ball-like cluster in the ascus. Usually there are eight ascospores, but sometimes there may be four and in some cases sixteen; rarely even as many as 512 have been reported. They are hyaline or coloured, one- or many-celled, or muriform.

Pathogenic forms, especially those attacking plants of economic

importance, occur in the families Ceratostomaceae, Mycosphaerellaceae, Gnomoniaceae and Valsaceae, but as the asexual state is the more prominent state on the living host and perithecia are formed only on dead tissues or in culture media, some of the more important diseases are dealt with under the orders Melanconiales and Sphaeropsidales, of the class Fungi Imperfecti. Pathological usage has made the imperfect state, such as *Colletotrichum*, *Ascochyta*, *Cercospora*, the more popular, for the perfect states occur only as exceptions. Only one disease, the ring-spot of sugar-cane, is described under this order.

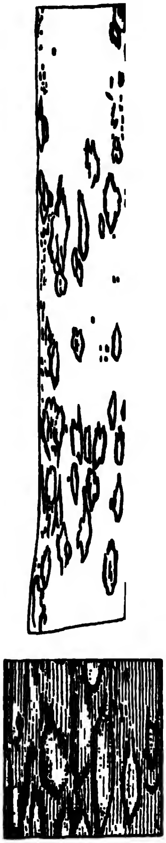


FIG. 85.—Ring-spot of sugar-cane, *Leptosphawria sacchari* (after Butler).

Ring-Spot of Sugar-Cane (*Saccharum officinarum* L.)

A leaf-spot of sugar-cane due to *Leptosphaeria sacchari* Breda de Haan is very common on the crop in several parts of India, especially the United Provinces, Madras, Bengal, Assam, and possibly Bombay. The fungus attacks only the thick canes, but the disease does not kill the plant entirely though it reduces the vigour by injuring the leaf-surface, which may ultimately result in poor yield. The disease symptoms usually appear soon after the rains have commenced, when the plants are two to three months old. The earliest symptom is the appearance, on both surfaces of the leaves, of small, discoloured, and generally purple spots which, as they grow and expand at the margins, render the central portion dry (Fig. 85). The margins consist of narrow, reddish-purple or brownish bands, outside which there is sometimes a yellowish areola, merging into the green of the leaf. The centre of the spot is straw-coloured, dry and sharply marked off by the surrounding coloured ring. Small black points arranged in rows dot the dry, straw-coloured area. These spots are scattered over the whole or part of the leaf-blade and, by the union of the neighbouring spots, they increase in size. They are lobed or broken by angular projections and very irregular. When a considerable part of the leaf is affected, it dries up and withers prematurely.

Within the leaf-tissues there are fine, hyaline hyphae which directly enter the cells and kill them, causing the cell-contents to collect in a brown mass at the centre. Perithecia are formed on the upper surface in large numbers as tiny dots. They are arranged in rows between the finer veins and lie buried in the leaf-tissues, with their tips projecting.

Perithecia are almost spherical, about 140 μ in diameter, and contain numerous, clavate, slender asci between which are fine paraphyses. Each ascus contains eight ascospores arranged in a biseriate or even in a triseriate manner. Ascospores are elongated, 3-septate, the two central cells, especially the upper one, being thicker than the end cells. They are rounded at the ends, at first hyaline, but later become light brown.

It is stated that unfavourable conditions of environment predispose thick canes to attack by the fungus, but as the disease has not assumed serious proportions, no great importance has been attached to it and detailed studies have not been carried out. Control measures are, therefore, unknown.

HELOTIALES

This order consists mostly of saprophytes, but some species of the genera *Pseudopeziza*, *Sclerotinia* and *Ciboria* are parasites on economic plants. The ascocarp is an apothecium which is disc-, saucer- or cup-shaped and stalked or sessile. Ascospores are commonly one-celled, but septate ascospores frequently occur.

In the family Sclerotiniaceae the apothecia arise from a definite sclerotium or a stromatized portion of fungal tissue. The apothecia are usually brown, stalked, cuplate, funnel- or saucer-shaped. The ascus is inoperculate, commonly with eight ascospores which are unicellular, hyaline, smooth, ellipsoidal and slightly flattened at one side. The stroma is the organ for the storage of food. Most of the species are vernal in their fruiting habit, and they attack, in general, only mature or aged and declining organs such as leaves, stems and fruits. In many of the species flask-shaped, pycnidium-like fruit bodies, known as **spermogonia**, are produced on the surface of the stroma. These spermogonia contain many **spermatiophores,** on the tips of which **spermatia** are produced semi-endogenously. These spermatia function as male cells in the process of fertilization.

Stem-Rot of Patwa (*Hibiscus sabdariffa* var. *altissima* Wester)

In Bihar patwa plants left over for seed after the main crop is harvested for fibre usually suffer from a serious stem-rot. The disease generally appears in the first week of January, and the main crop, which is harvested for its fibre some time about the beginning of October, escapes it. The first evidence of the disease is the appearance of a brown patch on the main stem or branches of the inflorescence, about 6 to 10 feet above the ground. The portion of the stem above and below the patch is, however, healthy in appearance. The pallid colour slowly extends until the stem is completely girdled. As much as a foot or a foot and a half of the main stem may ultimately become affected (Fig. 86). The stem at the affected region is less firm to the touch and easily peels off into shreds. The floral axis and the stem below it are, as a rule, affected, but the discoloration does not reach the ground-level or the roots.

Examination of the affected parts with a hand lens reveals that the surface of the stem is covered by cottony strands of the fungous mycelium, forming cushions at the junction where the axis of the branches meets the main axis (Fig. 86). Sometimes black, irregularly round bodies can be seen on the surface of the stem, and if the mycelium has spread to the bolls, they can also be seen in that region. Several bolls when opened have shown the presence of these black bodies, which are the sclerotia of the fungus.

The fungus responsible for stem-rot is *Sclerotinia sclerotiorum* (Lib.) de Bary. Its large septate strands infest the cells both intracellularly and intercellularly and all the tissues of the stem are invaded. Hyphae may be from 9–18 μ across, and they are densely filled with protoplasm. The pith region of the host may often be filled with sclerotia of the fungus. Sections of sclerotia show that they are composed of thin-walled rectangular cells in the centre, and thick-walled cells at the periphery. The walls of the latter cells are impregnated by a gelatinous material which gives these bodies their black appearance.

Experiments conducted at Pusa have shown that the mycelium of the fungus is unable to infect the plants, only the ascospores being capable of attacking the tender tissues of the host. Apothecia arise from the sclerotia if the latter are exposed to low temperature and then placed in bright light. Under the conditions prevailing at Pusa, the sclerotia of the previous season are not subjected to such a

low temperature until the following January, which is the principal reason why the disease manifests itself at that time and not before.

FIG. 86.—Inflorescence of *Hibiscus sabdariffa* attacked by *Sclerotinia sclerotiorum.*

When the apothecia appear, they eject the ascospores with considerable force, and those that land on the tender parts of the stem, which at that time are located only in the inflorescence, infect it.

The fungus over-summers, therefore, in the form of sclerotia, and danger starts only when they develop apothecia.

In devising control measures, this rôle of the sclerotia should be kept in mind and every effort made to destroy them. They may be, and in fact are, carried with the seed or they may lie in the soil. The former must be carefully hand-picked. In the case of soil infestation, the sclerotia should be prevented from forming apothecia. This can be achieved by deep ploughing and other means, so as to bury them deeply. As the parasite has a wide host range and attacks several dicotyledonous crops like *Brassica* species, *Helianthus annuus*, *Capsicum* species, *Sesamum orientale*, *Cicer arietinum*, etc., rotation with these crops is not helpful, but graminaceous crops may prove useful to some extent. Vernalization of seed for hastening flowering, and the development of early maturing varieties, would also help in achieving this object.

REFERENCES

ALLEN, R. F., " A cytological study of *Erysiphe polygoni* on *Delphinium*," *J. Agric. Res.*, **53**, 801–818 (1937).

BLACKMAN, V. H., and FRASER, H. C. I., " On the sexuality and development of the ascocarp of *Humaria granulata*," *Proc. Roy. Soc. Lond.*, B., **77**, 354–368 (1906).

BUTLER, E. J., " The leaf-spot of turmeric (*Taphrina maculans* sp. nov.)," *Ann. Mycol. Berl.*, **9**, 36–39 (1911).

CLAUSSEN, P., " Zur Entwickelungsgeschichte der Ascomyceten, *Pyronema confluens*," *Zeit. Bot.*, **4**, 1–63 (1912).

FITZPATRICK, R. E., " The life-history and parasitism of *Taphrina deformans*," *Sci. Agric.*, **14**, 305–326 (1934).

FRASER, H. C. I., " On the sexuality and development of the ascocarp in *Lachnea stercorea*," *Ann. Bot.*, **21**, 349–360 (1907).

GRAF-MARIN, A., " Studies on powdery mildew of cereals," *Memoir Cornell Univ. Agric. Exp. Sta.*, 157 (1934).

GWYNNE-VAUGHAN, H. C. I., and WILLIAMSON, H. S., " Contributions to the study of *Pyronema confluens*," *Ann. Bot.*, **45**, 355–371 (1931).

HARPER, R. A., " Sexual reproduction in *Pyronema confluens* and the morphology of the ascocarp," *Ann. Bot.*, **14**, 321–400 (1900).

MUNDKUR, B. B., " *Sclerotinia* rot of *Hibiscus sabdariffa* Linn.," *Indian Jour. Agric. Sci.*, **4**, 753–778 (1934).

SWINGLE, D. B., " Fertilization of *Ascodesmis nigricans* van Tieghem," *Amer. J. Bot.*, **21**, 519–541 (1934).

UPPAL, B. N., CHEEMA, G. S., and KAMAT, M. N., " Powdery mildew of the grape and its control in Bombay," *Bull. Bombay Dep. Agric.*, 103 (1931).

UPPAL, B. N., PATEL, M. K., and KAMAT, M. N., " Pea powdery mildew in Bombay," *Bull. Bombay Dep. Agric.*, 177 (1935).

CHAPTER VIII

BASIDIOMYCETES

THE class Basidiomycetes is characterized by its members possessing a well-developed mycelium which in the Hemibasidiomycetes is delicate and inconspicuous. The hyphae are multicellular and freely branched, and the mycelium is frequently perennial in the substratum, which may be wood, roots and stems of living trees, or humus of the soil. The mycelium living in the soil sometimes forms, in the Eubasidiomycetes, fairy-rings, sclerotia or rhizomorphs. Frequently it becomes transformed into wefts or woven into macroscopic structures of definite form and considerable differentiation of tissues, like the fruit bodies of the common mushrooms.

Asexual reproduction is by means of conidia, but the development which they attain in the Ascomycetes is not reached in this class except in the Uredinales, where they are common and form one of the chief methods for their quick dissemination. While asexual spores are borne on the haplont mycelium in the Ascomycetes, they are borne on the diplont mycelium in this class.

Many members of the Basidiomycetes, especially the Eubasidiomycetes, form **oidia**. They arise endogenously in a basigenous manner in chains, and whether formed on the haplont or the diplont mycelium, they are always uninucleate and haploid. On germination, they give rise to haplont mycelium.

Sexual reproduction is much reduced in the Basidiomycetes, and antheridia and oogonia are never formed. Despite their absence, an alternation of generations involving a change from a state where the mycelium is haplont to one where it is diplont, takes place. The basidium is formed on the haplont mycelium, and the sexual spores, which are basidiospores, develop at the apex. The nuclear phenomena accompanying these changes are rather complicated, and only recently have they been properly explained. Heterothallism is common, and basidia and basidiospores are never formed in heterothallic forms unless mycelia of opposite sexes are brought together. But, as in *Mucor*, there is no means of distinguishing morphologically the (+) and the (−) mycelia. Basidiospores contain a single nucleus with haploid number of chromosomes, and on germination, give rise

to haplont mycelium, which, in heterothallic forms, may be (+) or (—), depending on the nature of the basidiospore. This mycelium, if cultivated in a culture medium, will remain sterile and never form fruiting bodies. When, however, it is brought into contact with the mycelium of the opposite sex, sporophores and hymenium are formed. The diploid state is therefore a result of hyphal fusions between haploid mycelia of opposite sexes. Fusions may take place by the conjugation of two basidiospores of the opposite sex, or by the formation of tubular connections between the haploid cells and migration of the nucleus from one into the other cell, which thus becomes diplont.

The bringing together of the two nuclei of opposite sex does not mean that they immediately fuse and form a synkaryon. They merely lie side by side in close association for prolonged periods. Such pairs of nuclei are known as **conjugate nuclei.** When conjugate nuclei have to divide, they do so synchronously and pairs of daughter nuclei are formed, of which one pair becomes enclosed in one cell and the other in another cell, and by their repeated division in the same manner, millions of cells are produced.

In the Ascomycetes the binucleate cells of the ascogenous hyphae are without independent existence, but in the Basidiomycetes they are the normal vegetative mycelium and the mycelium of the fruiting bodies. Cells that contain a pair of conjugate nuclei are known as **dikaryotic cells** and the mycelium as **dikaryotic mycelium.** The process by which haploid mycelium is converted into dikaryotic mycelium is known as **diploidization**, and one cell is said to **diploidize** the other. Oidia which have a single haploid nucleus also give rise to a haplont mycelium which is also diploidized in the above manner. Oidia may act as direct diploidizing agents, for they are carried by wind or insects from mycelium of one sex to a mycelium of another, which they immediately diploidize.

The mycelium of the Basidiomycetes, especially in the Eubasidiomycetes, is characterized by the possession of clamp-connections which are not found in any other class. Clamp-connections occur only on the diplont mycelium, and it was at one time believed that they are connected with the diploidizing process, but it has now been shown that they merely help in the flow of protoplasm and food material from cell to cell through the pores in the septa. They are formed in the terminal hyphal cells and grow backwards, away from the apex and not forwards. As they occur only on the dikaryotic

mycelium, they are a visible sign of the presence of conjugate nuclei and an indication that the mycelium has passed from the haploid to the diploid state. However, while clamp-connections are always associated with conjugate nuclear division, the converse is not true, for such divisions may take place without their formation.

Mature dikaryotic mycelia produce basidia which are one- to four-celled, the young basidia being dikaryotic also. As they increase in size a fusion of the two conjugate nuclei, which has been so long delayed, takes place and a synkaryon is formed. Sometimes after its formation the synkaryon divides by a reduction division. This is followed by a second division, which is mitotic, four nuclei being thus formed, two of each sex. Later slender projections, known as **sterigmata**, develop at the distal end of the basidium on which basidiospores are produced, each with a single haploid nucleus. Basidiospores are oval, elliptical or spherical, smooth or echinulate, hyaline or coloured, and are also known as **sporidia**.

Basidiomycetes are divided into three sub-classes, depending on the manner in which basidia are formed. In one method a terminal cell of the dikaryotic mycelium forms a spherical structure known as a **chlamydospore**. This is the probasidium and forms a basidium (also known as a **promycelium**) on the germination of the former. This basidium may be septate or non-septate. Basidiospores are formed on sterigmata on the basidium and they may produce secondary spores by budding. In the second method the probasidium is known as a **teliospore**; this, on germination, develops a four-celled basidium, each cell of which produces a single basidiospore. There is, however, no budding. In the third method the basidium is formed directly on the terminal cell of the hypha. This is aseptate, and several such basidia are arranged in a palisade-like layer in the mycelium.

Basidia arising from a single probasidium, septate or aseptate, often irregular; basidiospores irregular in number, usually forming secondary spores by budding . . .	**Hemibasidiomycetes**
Basidia arising from a stalked probasidium, of strictly limited growth; septate and four-celled, each cell bearing only one basidiospore	**Protobasidiomycetes**
Basidia of strictly limited growth, aseptate, bearing a definite number of basidiospores, usually four	**Eubasidiomycetes**

There is a single order in the Hemibasidiomycetes, two in the Protobasidiomycetes and seven in the Eubasidiomycetes. Of these, representatives of Ustilaginales, Uredinales and Agaricales are discussed below.

USTILAGINALES

Ustilaginales are parasitic fungi, some species of which are facultative saprophytes. They are restricted to the flowering plants, but two species have been recorded on *Selaginella*, a pteridophyte. The **smuts**—by which name the diseases produced by these fungi are called—are characterized by the production on the host of dusty spore-masses which, as a rule, are deep brown or black, but some species, especially of the genus *Entyloma*, produce light-coloured, pale spots on the host and the spores are embedded in the tissues.

FIG. 87.—Jowar ear affected by long smut, *Tolyposporium ehrenbergii* (courtesy A. Ginai).

Hyphae are usually inconspicuous, local or widespread, hyaline and sparsely septate. They branch freely and are intercellular, but haustoria are present only in the Tilletiaceae. In some smuts the mycelium persists in the perennial parts of the host, though as a rule it becomes gelatinized and disappears.

The resting spore is the probasidium and is known as the **chlamydospore**, more commonly as a spore. In its development a cell at the apex of the hypha rounds off and envelops itself with a thick cell-wall which consists of an outer layer—the **epispore**—which is thick, pigmented, smooth or variously sculptured, and an inner layer—the **endospore**—which is smooth and delicate. Smut sori are formed in the ovaries, as in those of oats attacked by *Ustilago kolleri*, or in the anthers, as in those of *Dianthus* sp. attacked by

Ustilago violacea. They may destroy the entire flower, as in wheat attacked by *Ustilago tritici* (Fig. 89), or the whole floral axis, as in sugar-cane attacked by *Ustilago scitaminea* (Fig. 92). *Entyloma oryzae* causing the leaf-smut of rice, or *Urocystis tritici* causing the flag-smut of wheat (Fig. 23), form sori on the leaves, whereas *Uro-*

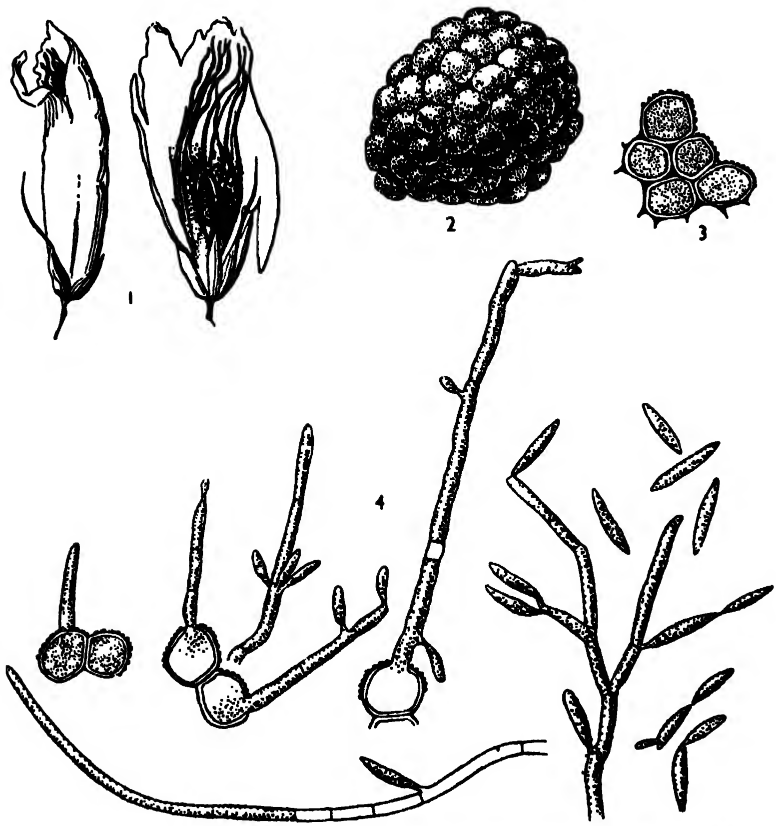


FIG. 88.—*Tolyposporium ehrenbergii* : *1* ruptured sori; *2* spore-ball; *3* part of same in section; *4* germination of spores (after Butler).

cystis brassicae induces gall formation in the roots of mustard (Fig. 33), *Brassica campestris.*

Chlamydospores are spherical to ovoid and one-celled, but sometimes several chlamydospores may become united into more or less permanent spore-balls. They germinate by the formation of basidia, also known as **promycelia**, and the classification of the order is

based on the nature of the basidium. If the basidium is septate, then the species are placed in the family Ustilaginaceae, and if unseptate, in the Tilletiaceae.

The promycelium of the Ustilaginaceae is long, hyaline and usually divided into four cells, each of which bears a basidiospore on a sterigmata. These basidiospores are known as **sporidia**. Sporidia when mature are abstricted at the base, and new ones may be formed until the protoplasm within the promycelial cells is exhausted.

Fig. 89.—Loose smut of wheat, *Ustilago tritici* : *1* wheat ears affected by smut ; *2* loose smut in fields.

Sporidia after abstriction bud like yeast cells. In some species, like *Ustilago tritici*, whose promycelium is four-celled, sporidia are not formed, but the promycelium gives rise instead to filaments, which are known as **infection threads** (Fig. 90).

The unseptate promycelium of the Tilletiaceae bears the sporidia terminally. In some species they become paired before or after falling off from the promycelium (Fig. 92, *2*). They are long and sickle-shaped and give rise to secondary sporidia.

Sexual reproduction is very much reduced in the Ustilaginales, though heterothallism appears to be rather common. Diploidization

is brought about by the fusion of pairs of sporidia which are haploid or of mycelial cells of the haplont mycelium, after which the dikaryotic phase begins. Sporidia are not differentiated morphologically, but they are apparently of two kinds. In *Ustilago violacea*, for example, two kinds of sporidia, which may be designated *A* and *B*, are produced on the same promycelium in approximately the same numbers, and fusion occurs only when sporidia *A* are brought into contact with sporidia *B*, and not otherwise. The development of two types of sporidia is determined by sex factors during the meiotic division of the synkaryon which is formed in the chlamydospore.

The method of infection of the host by the fungus is determined, very often, by the latter's chromosome constitution. In *Ustilago hordei*, for example, the germ-tubes of the sporidia are unable to gain entrance into the host because infection can be effected only by binucleate germ-tubes which arise from fused sporidia. In *Ustilago maydis*, however, the sporidia are able to infect the host even though they are haplont. But these haplont hyphae fuse in the host tissue, and thus become diploïd. As a general rule the fusion of two unisexual nuclei of opposite sex is prerequisite to normal infection and the production of the chlamydospores.

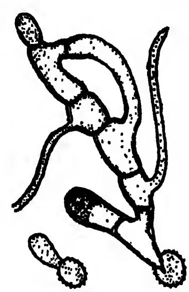


Fig. 90.—Germination of spores of *Ustilago tritici* (after Cunningham).

The order is divided into two families:

Promycelium septate, with lateral and terminal sporidia	**Ustilaginaceae**
Promycelium aseptate, with only terminal sporidia .	**Tilletiaceae**

The most important genera from the disease point of view are *Ustilago*, *Sphacelotheca*, *Tolyposporium*, *Tilletia*, *Neovossia*, *Urocystis* and *Entyloma*.

By causing disease in almost all our cereal crops and forage grasses, smuts inflict much damage. They fall into the following three groups as regards their manner of infecting the hosts:

(*a*) Chlamydospores externally associated with the seed and infecting seedlings.

(*b*) Chlamydospores not externally associated with seed; infection taking place at the time of flowering; chlamydospores

germinating on the stigma and sending their infection threads into the ovary, where they lie dormant in the embryo.

(*c*) Air-borne infection by sporidia through actively growing meristem.

The following key will be helpful in identifying some of the important smuts that attack crops in India.

***A*. Sporidia not produced**	
1. *Smut internally seed-borne*	
On wheat	*Ustilago tritici* (loose smut) (Fig. 89).
On barley	*Ustilago nuda* (loose smut).
***B*. Sporidia produced**	
1. *Smut externally seed-borne*	
On wheat :	
Spores smooth	*Tilletia foetida* (bunt) (Fig. 97, *1*).
Spores rough	*Tilletia caries* (bunt).
Spores many-celled, sori in leaves	*Urocystis tritici* (flag smut) (Fig. 23).
On barley	*Ustilago hordei* (covered smut) (Fig. 91).
On oats :	
Spores smooth	*Ustilago kolleri* (covered smut).
Spores echinulate	*Ustilago avenae* (loose smut).
On jowar :	
Spores amooth	*Sphacelotheca sorghi* (grain smut) (Figs. 93, 94).
Spores rough	*Sphacelotheca cruenta* (loose smut) (Fig. 95).
2. *Smut borne in setts*	
On sugar-cane	*Ustilago scitaminea* (whip smut) (Fig. 92).
3. *Smut air-borne*	
On wheat	*Neovossia indica* (Karnal bunt) (Fig. 97, *3* and *4*).
On rice	*Neovossia horrida* (black smut) (Fig. 99).
On bajra	*Tolyposporium penicillariae* (smut) (Fig. 96).
On ragi	*Melanopsichium eleusinis* (smut).
4. *Smut soil-borne*	
On jowar	*Sphacelotheca reiliana* (head smut).
On mustard	*Urocystis brassicae* (root-gall smut) (Fig. 33).

5. *Method of transmission unknown*

On rice	*Entyloma oryzae* (leaf smut).
On jowar	*Tolyposporium ehrenbergii* (long smut) (Figs. 87, 88).

The principal methods by which smuts can be effectively controlled are the following:

(1) Crop rotation and other cultural practices.
(2) Seed disinfection.
(3) Breeding resistant or immune varieties of crops.

Loose Smut of Wheat (*Triticum vulgare* Host)

Loose smut caused by *Ustilago tritici* (Pers.) Rostrup is fairly common in most of the wheat-growing tracts and manifests itself only when the plants are in ear. Diseased ears emerge out of the boot-leaf a little earlier than healthy ones, and a black, powdery mass of spores takes the place of the flowers (Fig. 89, *1*). The spores in young spikelets are covered by a silvery membrane which bursts before the emergence of the ear. Entire spikelets, with the exception of awns, are transformed into a powdery mass, and when spores are blown off only the central axis is left behind.

Spores, which are produced in great abundance, are pale olive, spherical to oval, 5–9 μ in diameter, and have minutely echinulate walls. On germination they do not produce sporidia (Fig. 90), but the promycelium gives rise to infection threads. When the spores fall on the feathery style of the wheat flowers, they germinate and produce promycelia from which arise infection threads which enter the style and grow forward intercellularly until the ovary is reached. By the tenth day successful entry is made into the ovule, where the germ-tubes branch and the mycelium becomes well ramified in it and in the embryo. The hyphae remain in the grain as dormant mycelium, which is thick-walled, oily and irregularly swollen. The dormant mycelium becomes active at the time the seed begins to germinate. The spores themselves are not viable for more than a few weeks under natural conditions.

As infection is internally seed-borne, external application of seed disinfectants is of no use whatsoever. In 1888 Jensen, a Danish investigator, found that if the dormant mycelium is induced to germinate, then it becomes vulnerable to heat, by the application of which it can be killed. Dormant mycelium itself, however, is very

resistant to heat. A method for controlling loose smut has therefore been devised based on these findings, and as now practised it is as follows. The seed is soaked in water at a temperature of 26–30° C. for four to five hours, which induces the dormant mycelium to germinate. The seed is then quickly transferred to warmer water at 54° C. for ten minutes, which helps in killing the germ-tubes. The thermal death points of the fungus and the seed are, however, near each other, and the margin of safety is thus very narrow. Extreme care has therefore to be taken in treating wheat seed against loose smut by this method.

A modification of the hot-water method has been devised in the Punjab, where summer temperatures, before the rains set in, are usually very high. The suspected seed is placed in shallow, flat-bottomed tubs and covered with water so that the water-level is about 2 inches above the level of the grain. The tubs are placed in the sun early in the morning and allowed to remain there for about five hours. At the end of the period the water is decanted and the soaked grain is spread on the threshing yard in the sun to dry. As a result of the action of the direct rays of the hot summer sun, the germinating dormant mycelium is killed and the seed is dried at the same time. The ease of operation makes it a superior method for controlling loose smut, provided the summers are long and very hot.

Immune or resistant varieties offer the best method of controlling loose smut. Investigations conducted at Delhi have shown that there are varieties of wheat, some of them with excellent agronomic and economic qualities, which are immune from or resistant to this disease. Their immunity or resistance has been tested from year to year by artificially infecting the ears, and has been maintained throughout.

Investigations conducted in Canada have shown that there are in *Ustilago tritici* at least six physiologic races which can be distinguished by their reaction on differential hosts. Such races complicate breeding programmes, for a variety immune or highly resistant to a race in one place may prove susceptible in another, with a different race. At the present time there is evidence to support the belief that there are only two physiologic races of loose smut in India.

Covered Smut of Barley (*Hordeum vulgare* L.)

Covered smut of barley caused by *Ustilago hordei* (Pers.) Lagerheim is prevalent in parts of Bihar, the United Provinces and the

Punjab, and is responsible for considerable damage to the crop. It first becomes recognizable when the blackened ears emerge from the leaf-sheaths. Every ear in a diseased plant and every grain in a diseased ear is generally attacked and turned into smut sori

FIG. 91.—Covered smut of barley, *Ustilago hordei*; *1* affected ear; *2* germinating spores (*1* after Butler).

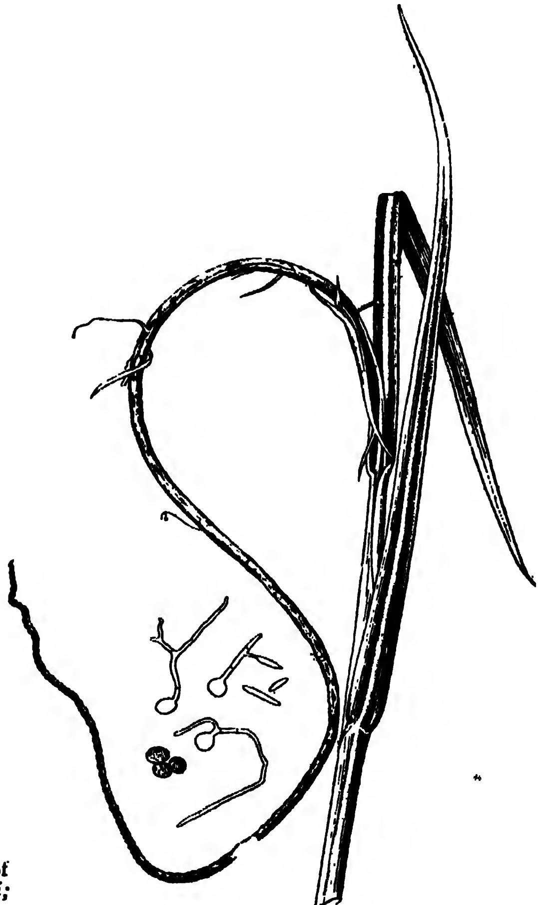


FIG. 92.—Smut of sugar-cane, *Ustilago scitaminea*, showing germinating spores (after Butler).

(Fig. 91, *1*). The ovaries are replaced by black spore-masses which do not fall apart as in loose smut, but are held together by the ovary wall and the glumes. In normal ears there are three spikelets at each joint of the rachis, but in smutted heads the lower halves of the spikelets fuse, the upper portions remaining distinct. As the spores

are firmly enclosed, they are not dispersed until threshing-time, when the ears get crushed, and the spores which are thus released adhere to healthy seed.

The spores of *Ustilago hordei* are globose to ellipsoidal, brown, though lighter coloured on one side, smooth, and up to 9 μ in diameter. They readily germinate in water or damp soil, producing short, stout promycelial tubes divided by septa into four cells (Fig. 91, *2*). Sporidia occur terminally and laterally and multiply by budding like yeast cells, even when detached.

Covered smut of barley is an externally seed-borne disease and can be effectively controlled by the use of fungicidal dusts such as Ceresan, Spergon, Agrosan, formalin dust or sulphur dust. Experiments conducted at Delhi have shown that sulphur dust that is capable of passing through a sieve with 300 meshes per linear inch or Agrosan gives excellent control.

Smut of Sugar-Cane (*Saccharum officinarum* L.)

The fungus causing sugar-cane smut was formerly known as *Ustilago sacchari*, but in 1924 Sydow, a German mycologist, stated that that name had actually been applied to a smut affecting the ovaries of some wild *Saccharum* spp., and was not the one that caused smut whips in sugar-cane. The fungus attacking the floral axis of this crop and turning it into a long whip was therefore renamed *Ustilago scitaminea* Sydow. There appear to be two other fungi that cause a similar smut, and their spores morphologically differ from those of *Ustilago scitaminea.* They have been named *Ustilago scitaminea* var. *sacchari-officinarum* Mundkur and *Ustilago scitaminea* var. *sacchari-barberi* Mundkur. The former has consistently larger spores with very large echinulations, while the spores of the latter are consistently smaller and are almost smooth. Sugar-cane smut occurs wherever sugar-cane is grown on a large scale, and is rather severe in water-logged and marshy places.

Affected plants are characterized by the production, at the growing axis, of a long, whip-like, dusty, black shoot often several feet in length and much curved on itself (Fig. 92). It is probably the floral shoot that is distorted, though the whip is found in varieties that ordinarily do not flower. The attacked shoot is devoid of leaves and is usually slender, flexible and covered by a silvery, thin membrane in its earlier stages.

The mycelium of the fungus infests the tissues of the cane below

the smut whip and is intercellular. The hyphae collect in dense masses towards the surface of the spore-bearing shoot where the spores are formed. As they are produced in great abundance, they rupture the silvery membrane, turning it off into flakes and shreds. The spores are echinulate, light brown, and 6·5–8·5 μ in diameter, and readily germinate in water or moist earth or air, producing a two- or three-celled promycelium from which terminal and lateral sporidia arise. Sugar-cane smut can be transmitted by the mycelium that is present in the setts from diseased clumps and also through the spores that are in the soil. Infection by spores at planting time is more common, but the incubation period in such cases is rather long, and several weeks may elapse before the symptoms become manifest. The disease therefore occurs late in the season when canes are approaching their full growth and maturity. Smut is more common in ratoon crops, and ratooning is, in consequence, usually discouraged.

Prevention rather than cure is the best method of controlling sugar-cane smut. In order to rogue smutted plants, a careful watch must be kept, and as soon as a whip is detected it must be carefully removed without allowing the spores to shed to the ground or the neighbouring canes. The plant itself must be uprooted and burnt, as it may be a potential source of infection. Such preventive measures help considerably in reducing the severity of the disease. There is no other method of directly controlling it. Attempts to obtain resistant varieties are under way at the experiment stations, and reports indicate that highly resistant canes have been discovered.

Grain Smut of Jowar (*Sorghum vulgare* Pers.)

Grain smut caused by ***Sphacelotheca sorghi*** (Link) Clinton is the most common and destructive disease of sorghum (jowar) in India, and losses caused by it, in regions where the crop is raised for grain for human consumption, are very severe. The smut affects the ovaries exclusively, and all the ovaries in a head are, as a rule, turned into smut sori (Fig. 93). It is not unusual, however, to find heads whose upper portion is unaffected while the lower portion is attacked. Infected ovaries are turned into greyish sacs which are enclosed by a wall made of fungous tissue (Fig. 94, *1*, *4*). The sori are one-sixth to one-half of an inch in length and up to one-sixth of an inch in width.

The sori are full of spores, but at the centre of the sorus is a slender column of hard tissue which is the **columella** (Fig. 94, *3*).

FIG. 93.—Grain smut of jowar, *Sphacelotheca sorghi*.

It is composed of tissues of the host plant and the fungous mycelium. Mixed with the spores are hyaline, empty, sterile cells. The spores are globose to oval, dark brown in mass but brownish-olive in-

FIG. 94.—*Sphacelotheca sorghi* : *1* sorus ; *2* columella after spores have fallen, *3* and *4* sori of same ; *5* to *10* promycelium and sporidia and budding of sporidia (after Butler).

dividually, smooth, and 5–9 μ in diameter. They germinate readily in water or nutrient solutions or moist earth (Fig. 94, *5* to *11*) and remain viable for more than five years. On germination they form a septate promycelium on which terminal and lateral sporidia are produced.

The smut is externally seed-borne, and spores attack the host

between the time of germination and the emergence of the seedling above the ground-level. The mycelium, once it enters the tissues within the host, follows its apical meristem. This invasion affects the metabolism of the growing plant in such a way that the host forms fewer nodes than does the normal plant. Infected plants therefore head earlier, and are also slightly dwarfed because of the reduction in the number of internodes.

FIG. 95.—*Sphacelotheca cruenta* : *1* sorus ; *2* spores showing echinulations ; *3* columella after spores have shed ; *4* various stages in germination of spores (after Butler).

As infection is externally seed-borne, seed-dressings effectively control grain smut. Organic mercury compounds and some non-metallic organic compounds have given excellent results, and it is possible to eliminate the disease totally. In India sulphur dust of extreme fineness is very popular because of its ease of application and cheapness. If the grain that is to be used for seed during the subsequent season is treated with sulphur immediately after it is threshed, then it is also protected against weevils and other insects.

Smut of Bajra (*Pennisetum typhoides* Stapf)

Bajra smut caused by *Tolyposporium penicillariae* Brefeld occurs in many more parts of India than was at one time believed. Only the ovaries are attacked, but not all of them in an ear are infected. The infected ovaries may be scattered or collected together in

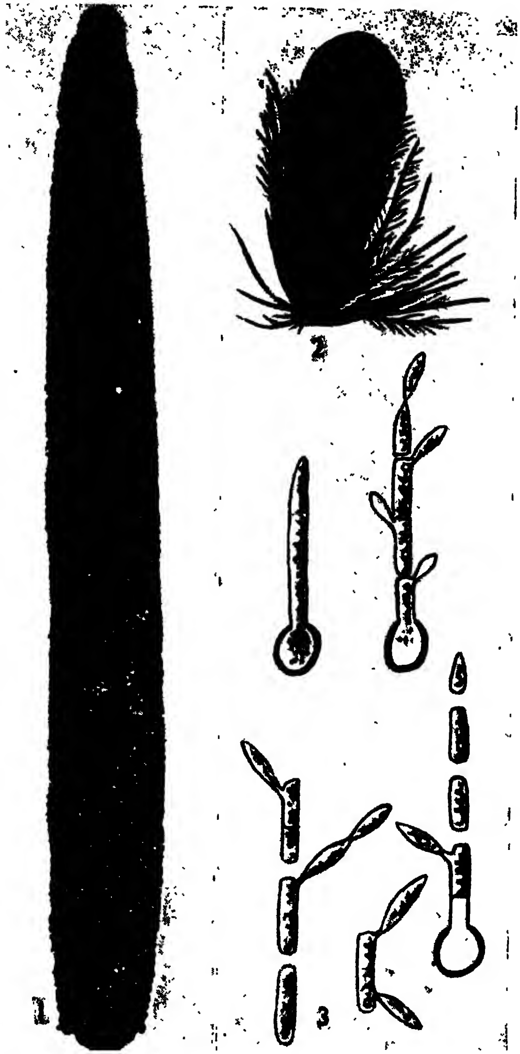


FIG. 96.—Smut of bajra, *Tolyposporium penicillariae*: *1* ear showing scattered sori; *2* a single sorus; *3* germinating spores (*2* and *3* after Butler).

patches (Fig. 96, *1*). Sori are oval to pyriform in shape, greenish when young and black when old, and twice the diameter of the normal grain (Fig. 96, *2*). They are covered by a tough membrane composed of host tissue and fungous elements; within the sori the spores

FIG. 97.—Bunts of wheat, *Tilletia caries* and *Neovossia indica* : *1* wheat ear attacked by rough-spored bunt; *2* germination of *Tilletia caries*; *3* wheat ears, bearded and awnless, attacked by Karnal bunt; *4* same as *3* but photograph of the ear.

are tightly pressed into balls which are more or less permanent and measure up to 150 μ in diameter. These balls break with difficulty even when placed in water. In each sorus there are thousands of such balls, but a columella is absent.

When the spores germinate they form a four-celled promycelium from which sporidia arise terminally and laterally. The promycelial cells have a tendency to break up into individual cells which fall off and continue to bud out sporidia (Fig. 96, *3*).

Bajra smut is air-borne. Spore-balls that have fallen to the ground germinate at the time the ears are about to flower, and give rise to numerous sporidia which are wafted by convection currents towards the floral axis, where they settle down on the flowers and immediately cause infection. A dormant mycelium, as in the loose smut of wheat, is not formed.

Seed treatment is not of any use in controlling air-borne smuts. Rogueing the smutted ears and destroying them by burning is a good preventive operation. There may be varieties of bajra that are resistant to this disease, and efforts to discover them seem desirable.

Bunts of Wheat (*Triticum vulgare* Host)

There are three principal bunts that affect wheat: rough-spored bunt, due to *Tilletia caries* (DC.) Tul. (formerly known as *Tilletia tritici*); smooth-spored bunt, due to *Tilletia foetida* (Wallr.) Liro (formerly known as *Tilletia foetans* or *Tilletia levis*); and Karnal bunt, due to *Neovossia indica* (Mitra) Mundkur. In India the first two bunts occur only in regions with a low temperate and a cool climate, and at elevations 6000 feet above sea-level. Karnal bunt is common in the plains, but occurs only in the Frontier Province, the Punjab and the Western Districts of the United Provinces. Elsewhere it is unknown.

These bunts attack only the grain, and they can be distinguished by the nature of the symptoms they produce. The first two—namely, the rough-spored and the smooth-spored bunts—are externally seed-borne and therefore systemic. Plants affected by them ripen a little earlier, and the ears assume a dark-green colour and are more open than those of the healthy plants. Bunted ears are, moreover, narrower and longer than the healthy ones and, as they mature, the glumes become pushed apart (Fig. 97, *1*) because the affected grains are plumper and shorter than the normal grains. In some varieties of wheat, bunt-balls are easily noticeable, but in others they can be

detected only with difficulty. As a rule, all the ears in a bunted plant are attacked, and all the grains in an ear are turned into bunt-balls, though exceptions occur. Sometimes a few of the tillers may be unaffected, but it is rarely that one finds ears which are only partially bunted. A careful examination of such partially bunted ears shows that the bunt-balls are not distributed irregularly in the ears, but occur in a regular manner, one above the other. In some cases only one side of the ear may be attacked, while the other is healthy. If a mature bunt-ball is squeezed, it will burst open, exposing a greasy, dusty powder composed entirely of spores and smelling strongly of rotten fish.

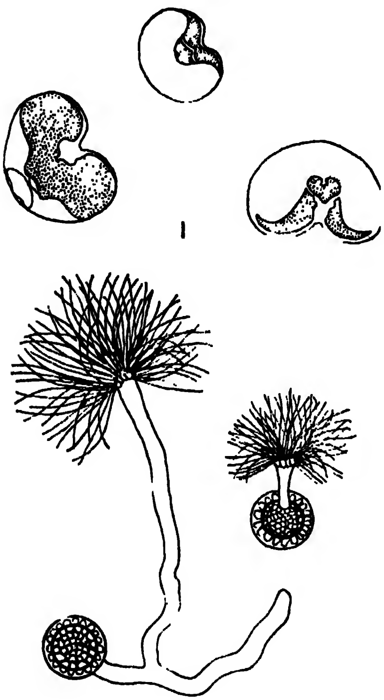


FIG. 98.—Karnal bunt of wheat, *Neovossia indica*. sections of wheat grain, partially attacked by *Neovossia indica*; *2* germinating spores with numerous sporidia.

Spores of both these bunts are more or less alike, excepting that those of *Tilletia caries* have a reticulate wall and a slightly smaller diameter, 15–20 μ, as against the smooth wall and larger diameter, 16–25 μ, of *Tilletia foetida*. Both the bunts may occur in the same stool and even in the same ear. Spores germinate readily in moist air or water, producing a stout promycelium which bears at its tips eight to fifteen narrow, curved sporidia. These sporidia, which are known as **primary conidia,** unite in pairs forming H-shaped structures (Fig. 97, *2*). Secondary sporidia are produced on short pedicels either directly on the H-shaped structures or on a fine mycelium which develops from them. These sporidia put forth hair-like infection threads.

Both the above bunts are externally seed-borne, and have therefore been effectively controlled by seed treatments. Copper carbonate dust, Ceresan, Agrosan, Spergon and other seed treatments have

been found to be very efficacious. The dusts must be of extreme fineness, and are applied at the rate of 2–3 oz. per bushel (60 lb.) of seed, using a seed-treating machine shown in Fig. 130.

The symptoms produced by the Karnal bunt are, however, totally different. In the first place, the disease is not seed-borne and there is no evidence of fungal attack in the plants until the grains are formed. In an infected plant not all the ears in a stool show infection, and in an attacked ear only a few grains, not more than five or six, are turned into sori. The sori are not regularly arranged, nor do they occur on any particular side. They are thus very irregularly distributed, as they would be if infection is chance infection due to air-borne sporidia, and not systemic infection (Fig. 97, *3*, *4*). Whereas in the other two bunts the entire grain is turned into a bunt-ball, in the Karnal bunt only two or three grains in an ear are so transformed, the remaining few being partially attacked (Fig. 98, *1*). As the grains mature, the outer glumes in a spike spread out slightly and the inner glumes expand, with the result that the bunted grains can be detected if carefully examined, but not otherwise. The bunt-balls are at first enveloped by the pericarp, but this later bursts and the spore-mass lies exposed. The spores emit the same kind of odour as the other two bunts.

Spores are darker brown than those of *Tilletia caries* and *Tilletia foetida*, spherical to oval and 22–49 μ in diameter. Some of them are double the size of the spores of the other two bunts. They have reticulate outgrowths on the surface of the epispore, giving an impression of dark bands furnished with projecting curved spines. They are surrounded by a thin, hyaline membrane which persists until after maturity. This membrane is somewhat gelatinous. Mixed with the spores are numerous, large, yellowish sterile cells.

Spores germinate after a long rest period. If they are soaked in water for about ten days and then placed in moist air, they germinate by putting forth short and stout promycelia, at the apex of which 60–120 sporidia are formed (Fig. 98, *2*). They are long, sickle-shaped, and neither fuse nor form H-shaped structures. On germination they form infection threads which are capable of infecting the host. Infection takes place only in the flower-buds soon after the ears have emerged out of the boot leaves, and the threads are incapable of infecting the ears at a later stage.

Seed treatment for Karnal bunt is out of the question, as the disease is not seed-borne. There are no other direct methods of

control. Efforts to develop varieties of wheat that resist the disease are likely to yield fruitful results.

FIG. 99.—Bunt of rice, *Neovossia horrida* : *1* photograph of affected ear; *2* germinating spore; *3* sporidia.

Bunt of Rice
(*Oryza sativa* L.)

The fungus causing bunt of rice was at one time placed in the genus *Tilletia* and named *Tilletia horrida*, but observations have shown that the spores germinate in a manner characteristic of the members of the genus *Neovossia*, and its precise name now is *Neovossia horrida* (Tak.) Padwick and Azmatullah. It is widely distributed in Assam, Bengal, and in the United Provinces, where it has been reported to occur as an epiphytotic in certain years. Only a few grains in an ear—not more than three or four—are affected and, as in Karnal bunt of wheat, not all the ears in a stool show the presence of bunt-balls. In a majority of cases the sori are hidden by the glumes, but sometimes they have been known to force the glumes apart slightly and black masses of spores are extruded (Fig. 99, *1*).

Spores are spherical and black when mature and measure 20–24 μ in diameter. The epispore is provided with spines or blunt pegs and surrounded by a thin, hyaline membrane which persists until

after maturity. Spores are adhesive because the hyaline membrane becomes gelatinous when moistened, and they germinate if they are soaked in water for about ten days and then placed in moist air. They put forth short and stout promycelia on which eighty or more sporidia are formed (Fig. 99, *2*). Sporidia do not fuse or form H-shaped structures.

Infection takes place when the ears have just emerged out of the leaf-sheaths. Sporidia from the germinating spores are carried by the convection currents and settle down on the flowers, especially young styles, sending out germ-tubes into the developing ovaries, where the fungus finally settles down, outside the aleurone layer or under the wall. Sori are formed in maturing grain, where an extensive cavity develops between the seed-covering and the endosperm, the hyaline mass ultimately replacing starch cells. Spores start to develop very soon thereafter, beginning as thin-walled swellings on short branches.

As only a few ears in a stool and not more than three or four grains in an ear are attacked, the disease has attracted little attention and not caused widespread havoc. It was formerly believed to be seed-borne and seed treatments were tried to control it. It is now known to be air-borne, and seed treatments are therefore useless. No other measures of prevention are known.

Among members of the Tilletiaceae, *Urocystis tritici* Koernicke causes the flag smut of wheat (Fig. 23) and *Urocystis brassicae* Mundkur the root-gall smut of mustard (Fig. 33, *2*). The former is an externally seed-borne smut, and can be successfully controlled by the use of seed dressings. The latter is soil-borne, and methods for controlling it are not yet known. Both these smuts are very much restricted in their distribution; the former occurs in the Punjab and the North-West Frontier Province, and the latter only in Bihar.

UREDINALES

Uredinales or rusts are obligate parasites capable of existing on living green plants, principally conifers and flowering plants. The order is very important from an economic point of view, and has about 130 genera and over 3000 species, some of which cause enormous losses to cereal and other crops. Much research has been done on the rusts, and many salient points in their life-cycles have been brought to light.

Mycelium is well developed, multicellular and moderately branched. There are, however, no clamp-connections in the diplont mycelium. There is very little diversity in its structure and the mycelium is principally intercellular, sending finger-like, globose, rarely convoluted haustoria into the host cells. In rare cases the mycelium is intercellular in the leaf parenchyma and intracellular in the epidermis. It may be localized or systemic: in the former case it extends to a short distance into the host tissues near the place of infection; but when it is systemic it induces the formation of galls, witches' brooms and other malformations in the host in which it perennates.

Reproductive structures appear after the mycelium has fully developed. The Uredinales are, as a rule, polymorphic, and different names have been applied to different stages, depending on their biological relationships and their behaviour: pycniospores (pycnidiospores), aeciospores (aecidiospores), urediospores (uredospores), teliospores (teleutospores) and sporidia (basidiospores). With the exception of sporidia, all other spore forms are borne in definite sori.

Pycniospores are borne in a pycnium which develops on the haplont mycelium, produced as a result of infection of the host by a sporidium. Pycnia are sub-epidermal or sub-cuticular and are the precursors of, or associated with, the other spore-forms, usually aeciospores. They are lenticular or flask-shaped and have an ostiole. Slender sporophores arise from the pycnial hymenium from the apex of which the pycniospores are cut off (Fig. 100). Pycniospores are uninucleate and haplont.

The function of pycnia and of pycniospores was for a long time a matter for speculation. They were once considered to be functionless male cells, but an important discovery made in 1927 by Craigie in Canada indicated that the pycniospores are haploid bodies of (+) or (—) sexes. He demonstrated that *Puccinia graminis* is heterothallic and that the four sporidia arising from a teliospore are of two sexual groups. If a single sporidium from the germinating teliospore is sown on a barberry leaf, the resulting pycnium is either (+) or (—) in its sexual tendencies. If such a pycnium is not allowed to intermingle with another of the opposite sex, aecia fail to develop; they arise only when the contents of (+) pycnium are brought into contact with the contents of a (—) pycnium and *vice versa.* A vertical section through the barberry leaf shows that the pycnium is sub-epidermal and consists of a wall bearing several pycniosporo-

phores from which the pycniospores are cut off, and of a chamber into which they are set free. From the ostiole of each pycnium a drop of nectar is excreted, which by its scent and sugary content is attractive to insects which help in the mingling of the pycniospores of the opposite sexes. The pycnium sends into such nectar numerous paraphyses and a small number of slender and branched hyphae known as **flexuous hyphae** (Fig. 100, *1*). After the mixing of the pycnial nectar, a fusion between the pycniospores and flexuous hyphae takes place. In the meanwhile the haplont hyphae similar to those from which the pycnia arose mass together in a substomal

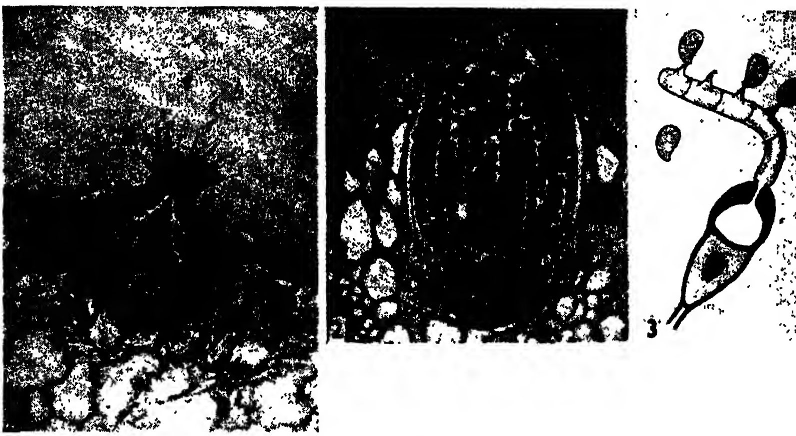


FIG. 100.—*1* Pycnium and flexuous hyphae of *Puccinia graminis*; *2* aecia of same; *3* germinating teliospores (courtesy, Rust Research Laboratory, Winnipeg).

chamber or some other large intercellular space in the vicinity of the pycnium but on the opposite side of the leaf. Here the haploid rudiments of the aecial fructifications, known as **protoaecia**, are in the process of formation (Fig. 100). Protoaecia develop into aecia only when they are diploidized by the nuclei of the opposite sex that enter the flexuous hyphae and migrate towards the protoaecia.

In some species fusion between the pycniospores of one sex and the paraphyses that develop in the pycnia of the opposite sex, has been observed. Diploidization may also be brought about when the mycelia of opposite sexes meet and anastomose in the tissues of the host, bringing about a mixing of nuclei. The septa of the hyphal cells do not form barriers for the rapid progress of pycnial nuclei, and a single act of diploidization suffices to make it wide-

spread. In *Puccinia helianthi* the haplont hyphae of the monosporidial origin are known to anastomose with the uredial hyphae that are dikaryotic. The latter thus contributes to the former the nucleus which it lacked and diploidizes it. Such diploidization of a haplont mycelium by a dikaryotic mycelium is known as the **Buller phenomenon.**

The aecium is usually bell-shaped and enclosed by a one-cell thick wall, known as a **peridium** (Fig. 101). In cutting aeciospores, the uppermost cell with its daughter nuclei becomes the aeciospore

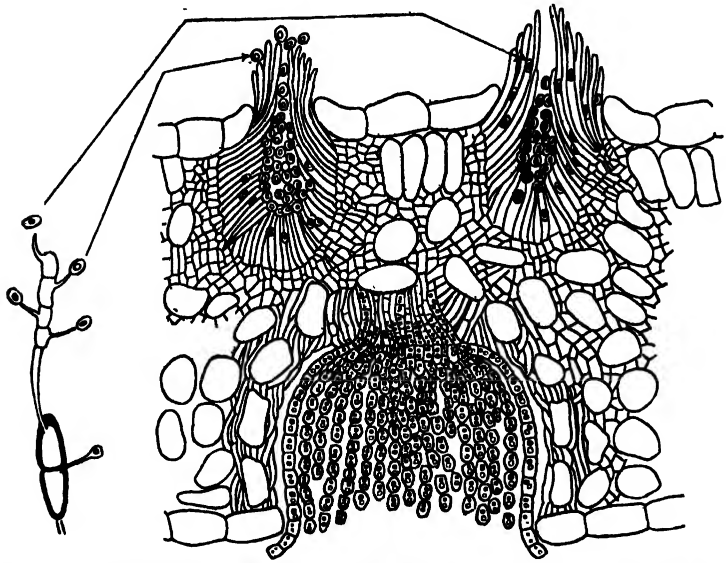


FIG. 101.—Diagrammatic representation showing indicating heterothallism in *Puccinia graminis* and formation of aecia.

mother-cell. This divides again, producing the aeciospores at the apex and an associated cell below, which is known as a **disjunctor-cell.** It is in fact a rudimentary pedicel for the separation of the aeciospores. The process of aeciospore and disjunctor-cell formation continues until a chain of spores is formed. Aeciospores remain viable for a time, and germinate when they fall on suitable hosts.

Germination of the aeciospores leads to the formation of a dikaryotic stroma within the host from the base of which grow short, two-celled upright branches. The upper cell becomes the urediospore and the lower the pedicel. The sori in which these uredio-

spores are formed may not have a distinct or definite shape, and are known as **uredia**. When the air is charged with moisture and is still, repeated production of urediospores takes place over a period of days. Urediospores are yellow to orange-red, globose or oval, binucleate, with their wall made up of two distinct layers. The endospore is provided with germ-pores whose number and position are of assistance in the identification of certain genera and species. The epispore is generally verrucose or echinulate and only rarely smooth. The urediospores are easily wafted by wind over long distances, and if they come into contact with a suitable host, they germinate and the germ-tubes penetrate the host through the stomata.

Towards the end of the growing season the formation of uredia ceases and teliospores begin to appear. At first they may be formed in the uredia themselves, but later they are formed in separate sori, the **telia**. The teliosporophores grow vertically from a hymenium and become the teliospore mother-cells. The latter divide into a lower cell which on elongation becomes the pedicel, and an upper cell which is the teliospore itself. The upper cell may undergo further division, producing two- to several-celled teliospores. The young teliospores are at first binucleate, but later the two nuclei fuse producing a synkaryon, when the dikaryotic phase comes to an end.

The morphology of the teliospore furnishes the principal characteristics for the differentiation of genera of the Uredinales. Teliospores are dormant spores, and germinate as a rule after a period of rest by the formation of a long promycelium which is usually four-celled. Each one of the promycelial cells is provided with a haploid nucleus formed as a result of two divisions of the fusion nucleus, the first being a reduction division. A single sporidium is formed on each of the promycelial cells on a short, pedicel-like structure, the sterigmata. Several deviations from this common method have been observed. Teliospores of *Catenulopsora* germinate without a rest period; those of *Melampsora* are sessile. Teliospores of *Coleosporium* form an internal promycelium (that is, the teliospore becomes four-celled, each cell being a promycelial cell).

The sequence of appearance of the spore-forms is strictly in the order given above (that is, pycnia and pycniospores, aecia and aeciospores, uredia and urediospores, and telia and teliospores). It is controlled by inherent internal factors and is never reversed. A spore-form may be, and sometimes is, omitted in certain genera and

species, but the order of appearance of sori is always the same. The spore-forms are designated by the following symbols:

O = Pycnia and pycniospores.
I = Aecia and aeciospores.
II = Uredia and urediospores.
III = Telia and teliospores.
IV = Sporidia (this symbol is generally not used).

Teliospores are produced by all the Uredinales. In the genera *Endophyllum* and *Kunkelia* they resemble the aeciospores and were formerly mistaken for them. On germination, however, they produce a four-celled promycelium. Such teliospores are known as **aecidioid-teliospores** or **micro-teliospores.**

Some rusts produce pycnia, aecia and telia, the uredia being eliminated from their life-cycle. The aeciospores or the teliospores then assume the rôle of summer or distributing spores. They are known as **opsis-forms.** Jasmine rust, *Uromyces hobsoni*, is an example of an opsis rust. It does not produce urediospores at all, and the aeciospores assume their function. Other rusts may produce pycnia, uredia and telia, aecia being eliminated from their life-cycles. These are **brachy-forms.** *Puccinia suaveolens* is such a rust, as it does not have an aecial stage. In some rusts only pycnia and telia occur, both the aecia and uredia being eliminated. These are **microcyclic** or **short-cycled** rusts. If all the spore-forms are present in a rust, then it is known as an **eu-form** (also **macrocyclic** or **long-cycled** rust). *Puccinia graminis* is a eu-form. In many rusts only uredia and telia are known, pycnia and aecia not having been discovered. These are **hemi-** or **demi-cyclic** rusts.

In addition to their obligate parasitism, rusts are restricted to particular host species, and are as a rule unable to attack other species of plants. That is, they show host specificity. *Puccinia sorghi*, for example, which attacks maize, is unable to attack jowar and is restricted to maize alone. *Puccinia purpurea*, which attacks jowar, is unable to attack maize. *Hemileia vastatrix* is restricted to coffee, and *Melampsora lini* to linseed. Some rusts, however, are able to attack very nearly allied species or species of closely allied genera. For example, *Puccinia graminis* can attack several species of the genus *Triticum* and also the genera *Hordeum* (*H. vulgare*), *Avena* (*A. sativa*) and *Festuca*, etc.

Rusts may be **autoecious** or **heteroecious** (that is, they exhibit

the phenomena of **autoecism** and **heteroecism**). In autoecious rusts all the spore-forms occur on the same host. *Melampsora lini*, which causes linseed rust, is an autoecious rust. Pycnia, aecia, uredia and telia occur on the linseed plant. On the other hand, in *Puccinia graminis* pycnia and aecia are produced only on barberry (*Berberis vulgare*), whereas the uredia and telia are produced on wheat. In other words, the sporidia that arise on the germination of teliospores of this rust are unable to infect wheat leaves, but can infect leaves of barberry. Aeciospores produced on barberry are in turn unable to infect barberry leaves, but only wheat leaves. The germ-tubes of both the sporidia and the aeciospores therefore show a

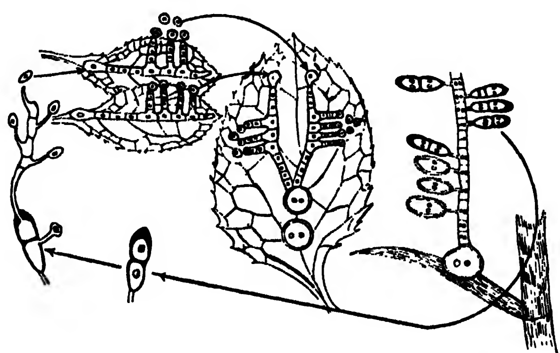


FIG. 102.—Life-cycle of *Puccinia graminis* diagrammatically represented, showing the mechanism of heterothallism (after Lehmann).

marvellous discrimination in their nutritional requirements. The graminaceous host which is able to satisfy the nutritional needs of the urediospores and the teliospores is unable to satisfy those of sporidia, which barberry is able to provide. Recently it has been reported that a barberry has been found in nature with all the four stages of *Puccinia graminis*.

Heteroecious rusts have two hosts, which are known as **alternate** hosts. They are widely separated taxonomically, and there are indications to show that a shifting of alternate hosts from the gymnosperms to the angiosperms is taking place. If the alternate hosts grow scarce or are absent from a locality, the existence of the rust becomes precarious and an abandonment of heteroecism may eventually take place. As a rule heteroecism is a characteristic of macrocyclic rusts. Most of the demicyclic rusts are apparently heteroecious

rusts, the alternate hosts of which have not been discovered. Finding the alternate host of a heteroecious rust is of much importance in rust studies. Sometimes it is possible to control a rust, to some extent, by eliminating the alternate host. Annual recurrence of wheat rust due to *Puccinia graminis* has been considerably reduced in the United States by a systematic eradication of barberries.

The order is divided into three families as follows:

Teliospores sessile, forming crusts or cushions or columnar masses in the mesophyll of the host	**Melampsoraceae**
Teliospores usually stalked, separate or held together in gelatinous masses; sometimes several on a common stalk; less commonly sessile; catenulate or breaking apart . .	**Pucciniaceae**
Teliospores unknown	**Uredini imperfecti**

MELAMPSORACEAE

Aecia in the family have a well-developed peridium, but in some genera and species it may be absent. The uredia may also be enclosed by a peridium formed of polygonal or tube-like cells, and in some genera paraphyses are also common. Urediospores are borne singly on pedicels, but teliospores are as a rule sessile. They are firmly combined into one- or many-layered crusts or columnar bodies, and in the majority of cases they are single-celled. Many-celled teliospores due to vertical septation are also known. On germination the teliospores form a free promycelium, but in *Coleosporium* the promycelium is internal.

Rust of Linseed (*Linum usitatissimum* L.)

Linseed rust caused by *Melampsora lini* (Pers.) Lèv. is prevalent in almost all the countries where the crop is grown on a large scale, and, as in India, the cultivation of this crop is greatly handicapped because of its periodical epiphytotics. In parts of the Bombay and Central Provinces it appears as early as the fourth week of December, but in the United Provinces and Bihar it is not in evidence before the end of January. Injury to the crop results from a reduction in the amount of foliage and by the utilization by the fungus of some of the food of the host plant.

Affected plants are very conspicuous in the fields because of the bright orange colour of the affected parts. This is due to the uredia, which are large and occur on both the surfaces of the leaves (Fig. 103, *1*). Small uredia may be surrounded by necrotic zones. At

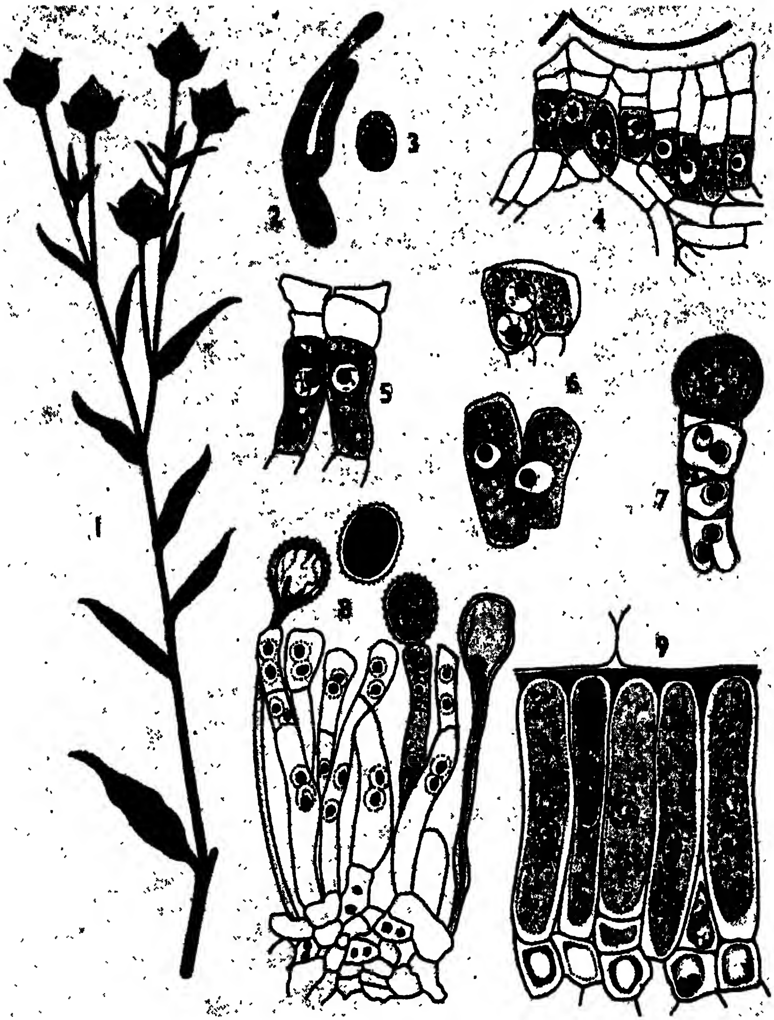


FIG. 103.—Linseed rust, *Melampsora lini* : *1* part of plant showing sori ; *2* branched sporophore from pycnium ; *3* a pycniospore ; *4* young aecium ; *5* paired cells of aecium ; *6* fusion of cells ; *7* formation of aeciospores ; *8* part of uredium with urediospores ; *9* part of telium with teliospores (*1* after Butler, *2* to *9* after Fromme).

first the leaves show only a little necrosis, but later it becomes more general and the leaves become chlorotic and die prematurely. As they are shed very early, there is scarcely any time for telial development on them, but reddish-brown to black telia are formed on the stems as black crusts.

Melampsora lini is an autoecious rust, all the four stages—pycnia, aecia, uredia and telia—occurring on linseed plants. It is also a long-cycled eu-form. Pycnia and aecia were not observed in India until 1940, when they were obtained in experimental cultures at Simla. In the northern parts of the United States it has been found that teliospores should be kept out during the winter months, when temperatures are as low as − 20° F. to − 30° F., before they can germinate normally in the following spring. The sporidia that arise from their germination attack young plants early in the season, producing small, inconspicuous, pale-yellow pycnia. They first appear on the upper surface of the leaves, but later on the lower surface also. They are flask-shaped, but may sometimes be a diffuse layer of pycniosporophores without a definite structure. The pycniospores are minute and oval to globose (Fig. 103, *3*). The aecia are orange-yellow, scattered on the under-surface of the leaves, and are without a peridium or paraphyses (Fig. 103, *4* to *7*). The aeciospores are polygonal, 17–27 μ in diameter, with a thin verrucose epispore.

Uredia occur on both sides of the leaves, scattered or in groups, and are usually circular in shape on the leaves (Fig. 103, *8*), but elongated on the stems. The spores are ovate, 15–25 μ in length and 13–18 μ in breadth, and provided with warts. Capitate paraphyses are abundant in the uredia with which the urediospores are intermingled. Telia are irregularly elongate, sub-epidermal, and form solid crusts which spread along the stems. They are not pustular. Teliospores are cylindrical, one-celled, 46–80 μ long and 8–20 μ broad. They are sessile, reddish-brown, and have a long dormant period (Fig. 103, *9*).

In the United States linseed which is grown for its fibre (flax) is sown in spring and harvested in autumn. The plants bearing the telial crusts lie in the open throughout the following winter, and the teliospores are thus exposed to the freezing temperatures. This enables them to germinate in spring, and the sporidia attack young linseed plants, initiating the epidemic. In India, where linseed is grown in the plains, it is sown in October and harvested in March.

Telia are exposed to the hot summer temperature and not to freezing temperatures, without which teliospores do not germinate. As the urediospores themselves do not retain their viability for more than a few weeks, their survival through the summer is most unlikely. How the annual recurrence of linseed rust is brought about has not, therefore, been properly explained.

The use of resistant varieties affords the only practical method of controlling linseed rust. There is a good deal of physiological specialization in the rust and, as such races occur in India, rust-resistant varieties have to be bred that resist the attack of as many races as possible. It has been found that the American and Australian flax varieties are immune under Indian conditions, and it may therefore be possible to obtain by hybridization varieties that are suitable for India and are completely resistant to the rust.

Rusts of Wheat (*Triticum vulgare* Host).

Three rusts are known to attack wheat—namely, black or stem rust due to *Puccinia graminis* Pers.; yellow or stripe rust due to *Puccinia glumarum* (Schmidt) Erikss. & Henn.; and brown or orange leaf rust due to *Puccinia triticina* Eriks. Of the thirty-three million acres under wheat in India, the bulk of the crop, amounting to nearly 95 per cent, is in the plains, the rest being on the hills. The crop is sown in October–November and harvested by the end of April or early May in the plains. In regions south of the Vindhya mountains harvesting may start in the fourth week of February, but on the hills it does not commence before June, and in Baluchistan and Kashmir the operations may last until the end of July.

Black rust (*Puccinia graminis* Pers.). In northern India black rust does not appear before March. As the crop by this time has reached the ' dough ' stage, the chances of its doing much damage are only slight. In the southern and peninsular India, however, it may appear as early as the fourth week of November, and losses to the crop from this cause are very severe (Fig. 104, *1*, *2*, *3* and *4*).

Uredia are the first to appear, and are very prominent on the culms, the leaf-sheaths, and also the leaves. The lesions are oblong and reddish-brown, and frequently merge into one another. As soon as they are mature, they burst, exposing the urediospores, which are brown in colour, oval in shape, and provided with a single thick wall with tiny spines and four germ-pores along the equator (Fig. 104, *3*). They readily germinate in water or moist air, forming

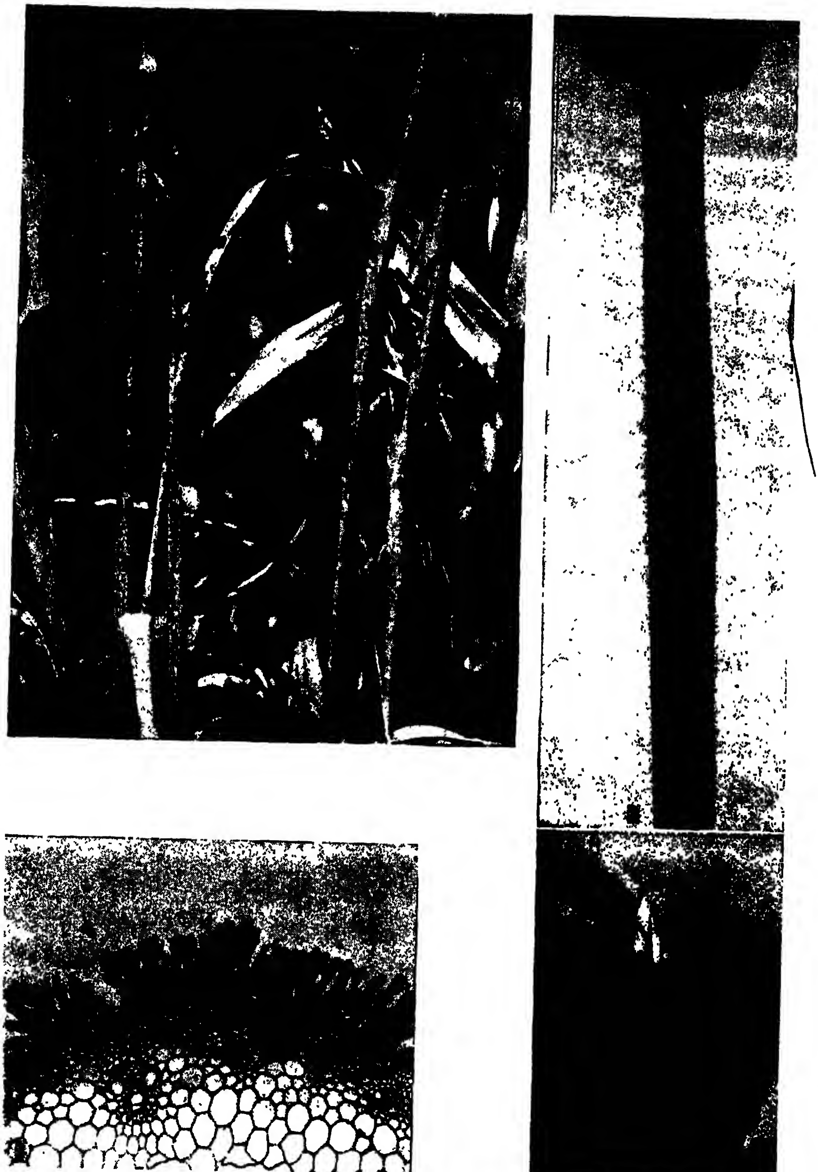


FIG. 104.—*1* Black rust on culms of wheat plants (courtesy E. C. Stakman); *2* same, enlarged; *3* telia and teliospores of *Puccinia graminis*; *4* inoculations of wheat seedlings with stem rust (courtesy, Rust Research Laboratory, Winnipeg).

germ-tubes that are capable of infecting wheat plants. Each sorus can produce hundreds of such urediospores, and the rust can therefore multiply readily and spread through the field causing severe epiphytotics.

Telia arise later in the season and develop principally in the leaf-sheaths and culms. They are conspicuous because of their oblong to linear lesions, dark-brown to black colour, and the teliospores exposed through the rifted epidermis. Teliospores are two-celled, chestnut brown, 49–60 μ long and 15–20 μ broad, and have a thick, smooth wall (Fig. 104, *4*). The apex is rounded, sometimes pointed, with a germ-pore through which the promycelium extrudes. The germ-pore of the lower cell is at the side, just below the septum. Teliospores have a long rest period, and before they can germinate they have to be exposed to freezing temperatures. On germination they form a long, four-celled promycelium. From each promycelial cell a sterigma grows on which roundish sporidia arise.

Puccinia graminis is a heteroecious rust, and its sporidia are unable to infect wheat plants. Several species of *Berberis* and the allied *Mahonia*, form the alternate host, the common barberry, *Berberis vulgaris*, being the most common. Wind-borne sporidia infect the young tissues of these plants, where the binucleate stage is initiated by sexual fusion. This phase is followed by the formation of the aeciospores (Fig. 102).

Pycnia are flask-shaped and consist of pycniosporophores and paraphyses with a pycnial chamber in the centre (Fig. 100). Pycniospores are cut off from the ends of the pycniosporophores. Pycnia may be (+) or (—) in their sexual tendencies, and the method of their fusion leading to the formation of aecia has already been described. Aecia are yellow, cup-shaped receptacles enclosed by a peridium (Fig. 101). The aeciospores, which are also yellow, are echinulate and provided with six germ-pores, and arise in chains from the base of the aecial cup. On germination they form germ-tubes which are capable of infecting only wheat (or some allied grasses), and not the barberry.

At one time it was supposed that the eradication of the alternate host would help in eliminating black rust, because of the incapacity of the sporidia to infect wheat, and of the urediospores, which do infect wheat, to survive the summer temperature of the Indian plains. It has now been discovered that urediospores serve as inoculum in a more general manner than was formerly realized. In Canada and

the United States it has been proved that in addition to the inoculum from the aecial host, urediospores that have formed on winter cereals and grasses in the southern United States and Mexico can be responsible for rust epiphytotics in the north. Eradication of the aecial host will not, therefore, be effective in eliminating rust, though it may play a more important rôle in reducing the development of the sexual stage of the fungus, and thereby preventing the production of hybrid strains, as hybridization takes place between different races in the aecial host, giving rise to new physiological races.

In India it has been conclusively proved that the fungus over-summers in the hills, at elevations of 5000 feet and above, where summer temperatures are congenial and where rust survives in the uredial stage on self-sown wheat plants. When the regular crop is sown, it is infected by this inoculum, and the infection then spreads gradually to the crop in the plains. Wheat is regularly grown in summer in the Nilgiri and Pulney hills in the south, where the uredial stage of black rust is thus able to survive.

The use of resistant varieties appears to be the only practical method by which black rust can be controlled. Elimination of wheat cultivation on the hills may help in reducing the severity of the epiphytotics, but there are other congenial grasses on which the rust over-summers, and the chances of its survival are thus not entirely ruled out. One such grass is *Briza minor*, which is wide-spread in the Nilgiri and Pulney hills. The parasite is segregated into several physiological races, and a variety resistant to one race may not be so to another. Occasionally severe losses occur when physiological races not common to the particular area suddenly appear and attack wheat varieties resistant to the existing physiological races. Resistance to black rust is governed by genetic factors which function for a group of physiological races of the parasite. In breeding of rust-resistant varieties all these facts should therefore be taken into consideration. In India there do not appear to be more than ten races, so far as at present known, and the success that has been attained in the development of varieties resistant to the existing physiological races indicates that black stem rust can be controlled.

Yellow rust (*Puccinia glumarum* (Schmidt) Erikss. & Henn.). This rust (Fig. 104 (*a*), *2*) is limited to northern and eastern India, being relatively rare in peninsular and western India. It appears early in January, and if there are heavy winter showers it is capable of doing much damage and inflicting considerable loss. Uredia are

chiefly confined to the leaves, but when the attack is severe they may appear on the leaf-sheaths, the stalks and even the glumes. Rust lesions have sometimes been seen on the pericarp of the kernels. As a result of attack by this rust the green colour of the leaves fades in long streaks on which rows of small uredia appear. In each row are a series of oval, lemon-yellow sori arranged end to end and each distinct from that above and below. The minuteness of the sori,

FIG. 104 (*a*).—*1* Brown rust, various degrees of attack (courtesy E. C. Stakman); *2* yellow rust (*a* urediospores, *b* teliospores, *c* shrivelled grain, *d* teliospores on glumes) (courtesy U.S. Dept. Agriculture).

their arrangement in linear fashion forming stripes, and their lemon-yellow colour, are the chief distinguishing macroscopic features of this rust (Fig. 24).

Urediospores are almost oval, and not round as in black rust, and their epispore is covered with fine spines. There are six to ten germ-pores, which are scattered, as against the four equatorial germ-pores of the black rust.

Telia are hypophyllous or culmicolous and occur in long, narrow

lines like the uredia. They are for a long time covered by the epidermis, with brown paraphyses surrounding the spores and intermingling with them along the edges of the telium. Teliospores are oblong to cuneiform, slightly constricted at the septum, and the apex is less thickened and pointed than in *Puccinia graminis*.

The rust is heteroecious, but as the alternate host is as yet unknown, the pycnial and aecial stages have not been observed.

The inoculum responsible for starting the annual epidemics comes from the hills, but whereas the black rust is able to over-summer at an elevation of 5000 feet above sea-level, *Puccinia glumarum* appears to require a still cooler temperature and therefore over-summers at still higher elevations, viz., 7000 feet and above. The further sequence of events that lead to the spread of the disease from the hills to the plains is as in black rust.

The adoption of varieties of wheat resistant to yellow rust is the most practical method of controlling it. Varieties that are less susceptible have been developed in India. As with black rust, there are physiological races of *Puccinia glumarum*, of which about ten are known in India. Varieties of wheat have to be resistant to a majority of them for successful control, if epidemics are to be avoided.

Brown rust (*Puccinia triticina* Erikss.). This rust (Fig. 104 (*a*), *1*) though more general in its occurrence, is more common in northern and eastern India than in peninsular India. It is perhaps the earliest rust to appear in certain parts of Bihar, Punjab and the United Provinces, and together with the yellow rust causes much loss and damage.

Uredia are, as a rule, confined to the leaves, being less common on the leaf-sheaths and stalks, and they are never in rows or stripes. They are round to slightly oblong, orange in colour and irregularly scattered or in clusters on the leaf-blades. The irregular arrangement of the sori and their orange colour form the most distinguishing features of brown rust. There are only three to four germ-pores on the urediospore wall, and they are scattered over the surface.

Telia are formed only rarely, and in some years they may not be present. If found at all, they are small, oval to linear, black, and covered by the epidermis. Paraphyses, which are abundantly present, divide the sorus into numerous compartments. The teliospores are oblong to cuneiform, slightly constricted at the septum, and the apex is rounded with prominent thickening.

The alternate host of brown rust occurs on species of *Thalictrum*, especially *Thalictrum flavum*. Their rôle in causing the annual outbreak of brown rust in India has not been precisely determined and does not seem to be important. The rust persists in the uredial stage on self-sown wheat plants in the hills at 5000 feet and above, as in the other rusts on wheat. Even in the case of this rust, the use of resistant varieties appears to be the only satisfactory way of controlling it. The fungus is segregated into numerous physiological races, of which eight are so far known in India. Varieties of wheat that are resistant to these physiological races have been discovered, and their extensive use would do much to bring this rust under control.

Rust of Beans (*Phaseolus vulgaris* L.)

Bean rust caused by *Uromyces appendiculatus* (Pers.) Link is widely distributed in India, especially in localities where there is a high relative humidity during the time the beans are in the field. It attacks several species of the genus *Phaseolus* (*Phaseolus mungo*, *Phaseolus radiatus*), but the damage caused is not very great. Sori occur on the leaves and pods, and very rarely on the tender parts of the stem and branches. They are most abundant and conspicuous, however, on the leaves, on which infection is usually most prominent on the lower surface (Fig. 105, *1*).

Uromyces appendiculatus is an autoecious rust, but the pycnial and aecial stages are not very commonly formed. Pycnia, when they do occur, are epiphyllous, but aecia are hypophyllous and cupulate. Aeciospores are ellipsoid, hyaline and minutely verrucose. Uredia are amphigenous, cinnamon brown, minute, almost white, and are slightly raised. Under favourable conditions they manifest themselves within five to six days after the spores have been applied to the leaf-surface. Urediospores are spherical to ovate, light brown, echinulate, and provided with two equatorial germ-pores (Fig. 105, *2*). Telia are amphigenous, rather small, and surrounded by a yellow band on the upper surface. Their production is governed by the age of the leaves and the physiological condition of the host. Teliospores are sub-globose or ovate, chestnut-brown, one-celled, thick-walled, and have a very slightly warty epispore (Fig. 105, *3*). At the apex is a large, hemispherical, hyaline papilla. They have a long resting period, which can, however, be shortened by storing them at freezing temperatures.

Urediospores, which are produced in great abundance, are responsible for the rapid spread of the disease and for causing epiphytotics, but the annual recurrence is brought about by the teliospores which carry over the organism from year to year. They preserve their viability in the soil debris until the following season, when they germinate and initiate the disease.

Dusting with sulphur or spraying with Bordeaux mixture, at frequent intervals, has given satisfactory control. It is, however, useless to apply the dust or the spray after the rust has become established, and it should not be done after the flowers have opened, as both these fungicides prevent seed setting in the pods. It is advisable to start dusting or spraying as soon as the primary leaves have unfolded, and continue it at weekly intervals thereafter. If the operation is done thoroughly, effective control can be obtained. The finer the sulphur dust, the better the control.

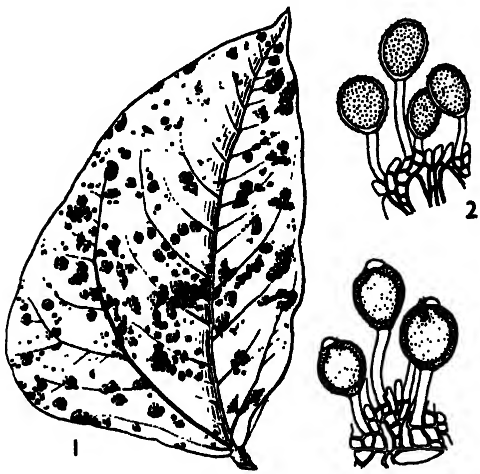


FIG. 105.—Bean rust, *Uromyces appendiculatus* *1* bean leaf affected by rust; *2* urediospores *3* teliospores (after Butler).

Varieties of beans resistant to rust have been produced in the United States. There are several physiological races of *Uromyces appendiculatus*, which has made the task of breeding resistant varieties rather complicated.

Leaf Rust of Coffee (*Coffea arabica* L.)

Leaf rust of coffee caused by *Hemileia vastatrix* Berk. & Br. was first recorded in India in 1870, and has become well established throughout the coffee areas of peninsular India; it has thus remained a major limiting factor in coffee production. It was first discovered in Ceylon in 1868, but it spread with such rapidity throughout the island, and caused such a great deal of damage, that an acre of land which yielded about four and a half hundredweights of coffee in

1870 gave only about two hundredweights in 1879. As a result, coffee cultivation became unprofitable and yields shrank so rapidly that the planters destroyed their remaining coffee-bushes and replanted their plantations with tea. Coffee rust is thus a classic example of a fungous disease completely altering the economy and prosperity of a country.

The disease is restricted to the leaves (Fig. 106, *1*), but rust sori have sometimes been seen on the berries and on tender shoots. The

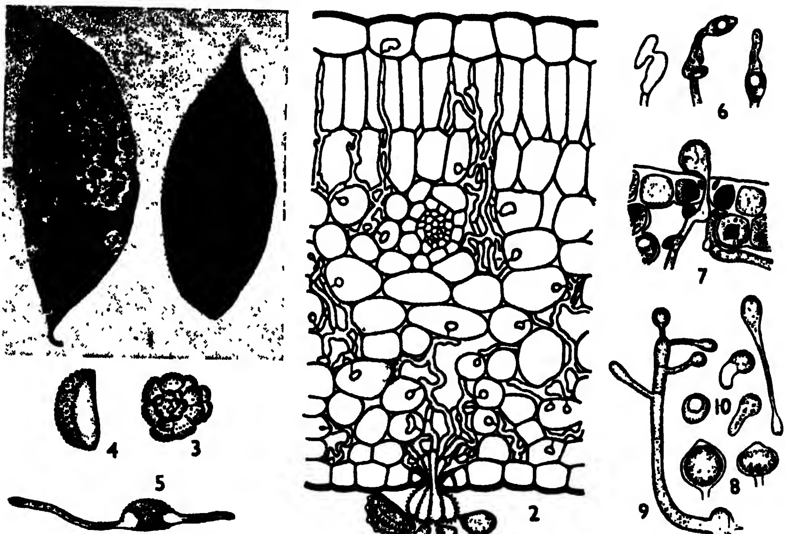


FIG. 106.—Coffee rust, *Hemileia vastatrix* : *1* leaves of coffee attacked by rust; *2* section through an infected leaf showing mycelium, haustoria and spore cluster; *3* a spore cluster seen from below; *4* and *5* a urediospore showing germination; *6* appressoria; *7* infection through stoma of leaf; *8* and *9* teliospores and their germination; *10* sporidia and their germination (*2* after Zimmermann; *3* after Delacroix; *4* to *10* after Marshall Ward).

rust is hypophyllous, appearing as small spots, 1–2 mm. in diameter. The spots are yellowish to begin with, but as they become more intense and increase in diameter they become orange in colour. Livid or brownish patches appear on the upper surface of the leaves, corresponding to the spots below. In severe cases of attack the entire leaves may turn brown and dry up.

Plants in all stages of growth are attacked, but young leaves are more susceptible to infection than mature ones, whose tissues apparently acquire resistance to invasion by the fungus. The

attacked leaves are shed in large numbers, and as the nutrition of the plant is seriously interfered with, a diminution of the crop is the result. The berries in such cases remain small and fail to ripen, and loss in yield up to half the estimated crop is not uncommon. As the yields fail progressively, the cultivation of coffee becomes very unprofitable.

Pycnial and aecial stages of *Hemileia vastatrix* have not been discovered, and it is not certain whether the rust is autoecious or heteroecious. Sporidia arising from the teliospores on germination are unable to infect the leaves of coffee, but extensive tests are desirable. It seems unlikely, however, that the rust is autoecious.

The mycelium is intercellular within the host tissues and provided with haustoria which penetrate the cells of the host as little swollen sacs (Fig. 106, *2*). At the time of urediospore formation, hyphae collect in the intercellular chambers below the stomata, and bundles of closely adherent stalks emerge from the mycelial masses through the stomatal opening (Fig. 106, *2*). After emergence the stalk swells into a hyaline enlargement which is cut off by a septum and becomes the urediospore. New urediospores arise from the same stalk lower down, each stalk thus producing several urediospores and becoming something like a swollen basal cell. Urediospores are not shed immediately, but remain attached to the tip of the pedicels by short sterigmata. In a mature uredium the pedicels lose their individuality and form a compound column, at the end and sides of which a densely crowded mass of sterigmata carries the spores.

Mature urediospores resemble the segments of an orange (Fig. 106, *4*). They are bifacially ovate or reniform, the upper side being convex and coarsely aculeate, the lower side flat or slightly concave, 26–40 μ long and 20–30 μ broad. Teliospores arise in the same sorus. They were once stated to be rare, but, after careful search, have been extensively collected in Ceylon and Mysore. They are mixed with the urediospores and arise from a basal cell like the urediospores. They are angular-globose, or turnip-shaped (Fig. 106, *8*), sometimes broader than long, and have an apical papilla. Their surface is smooth and the wall hyaline, but the contents are orange. They are 18–28 μ long and 14–22 μ broad and germinate without a rest period, *in situ*, by the formation of a narrow, long promycelium (Fig. 106, *9*). Rusts whose teliospores germinate without a rest period and *in situ* are usually autoecious, though there are exceptions.

A great deal of work on this rust has been done in southern India

by the Mysore Department of Agriculture and by the scientific officers of the Planters' Association. Careful observations made on the relation of the weather to the development of the disease show that shelter from wind, intermittent rain, dew or mist, ample light, very light overhead shade, and moderately high temperatures favour severe attacks. If the dry weather preceding the monsoon is short, and if there is much mist and dew during the dry months, then rust epiphytotics during the monsoon and subsequently may be very severe.

Spray schedules must be made, keeping the meteorological conditions in mind. If the dry-weather period has been brief and there have been showers in February, then the rust, as already pointed out, is most likely to be very severe. Spraying should start early in areas which carry a heavy head of leaf through the dry weather, when the new leaves are about a month old. But in places where the trees carry a small head of leaf through the dry weather and the initial source of urediospores at blossom time is slight, then the leaves may be allowed to mature before spraying starts. Bad timings may result in failure of sprays and waste of materials.

Efforts are now being made in Mysore and Coorg to secure varieties of coffee resistant to leaf rust. As a rule, *Coffea robusta* appears to be less susceptible than *Coffea arabica*; but the former does not yield coffee of as good a quality as the latter. A variety of coffee known as 'Coorg' was strikingly resistant on its first introduction in the 1880's, but its resistance was not maintained, and from the 1920's another variety, 'Kents', has proved superior, although not completely resistant to attack.

Studies at the Coffee Experiment Station in Mysore have shown that the differences in behaviour between 'Kents' and 'Coorgs' are due to the existence of physiological races of *Hemileia vastatrix*, of which four are present. Varieties of coffee that can resist these races are being developed at the Station, and the distribution of the races in Mysore and Coorg is also being ascertained. In the Cameroons a rust of coffee which produces a different set of symptoms and whose morphology is also different has been described as a new species, *Hemileia coffeicola* Maublanc & Rogers, but its distribution appears to be strictly limited to that country.

While coffee cultivation was exterminated in Ceylon by leaf rust, it still persists in southern India, mainly owing, it is suggested, to two reasons. After the south-west monsoon and the brief north-east

monsoon there is a long period of dry weather. The suggestion is that during this interval the defoliation of infected leaves continues, and as drought inactivates the fungus and there is not any leaf-tissue for it to infect, there is a gradual reduction in the source of inoculum. In Ceylon, on the contrary, there is no such well-marked or prolonged dry season, and the hot weather conditions remain favourable for the growth of the fungus, which thus remains in an active state. But at the same time there is in the Central Provinces an area in Berar, namely, Chikladha, where there are small coffee plantations. The rainfall here is less than 35 inches in a year, and the dry weather extends over a longer period than on the Western Ghats, where most of the cultivation of coffee in southern India is carried on. Nevertheless, leaf rust appears annually in a very destructive form at Chikladha, showing that the above explanation for the survival of coffee cultivation in southern India is not so simple as has been suggested.

In southern India coffee has been grown consistently under a canopy of shade which is practically continuous and is composed of a mixed stand of shade trees. This canopy affects the disease directly by checking spore distribution and by reducing light intensity, which in its turn checks urediospore production. This factor may also have contributed towards the survival of the cultivation in that area.

EUBASIDIOMYCETES

The sub-class Eubasidiomycetes is characterized by a true **basidium** and is represented by the mushrooms, toadstools, bracket fungi, puff-balls, bird's-nest fungi and stink-horns. The mycelium of the majority of the members of this sub-class is hidden within its substratum, the structures that are seen above ground or on the surface being the **sporophores**. The mycelium is dikaryotic or diplont, and clamp-connections, characteristic of such mycelium, are abundant.

Asexual spores do not attain the same varied development as they do in the Phycomycetes or the Ascomycetes. Sexual reproduction takes place in the basidia, where two nuclei which are conjugate, fuse to form a synkaryon (Fig. 107). Later the synkaryon divides twice, the first division being a meiotic division and the second mitotic. Four basidiospores on slender terminal outgrowths, the **sterigmata**, are then formed, into which a nucleus moves. The basidiospores in

this sub-class are as a rule unicellular, though in the *Dacrymyces* they may be transversely septate.

Basidia form a more or less palisade-like hymenium, and mingled with them in the hymenium are numerous enlarged sterile cells, the **cystidia**.

Sporophores are of three kinds. In the simplest case the fructification is a thick hyphal mat which grows radially in a definite manner, bears the hymenium on the lower side, and differentiates new hyphae and basidial elements at the periphery. This type of fructification is known as **resupinate**. From these simple types more complex forms for the increase of the surface over which the hymenium may be spread, are developed. This increase of surface may be secured by folds, wrinkles, formation of shelves, or by raising the hymenium on the surface of cylindrical clubs which may be much branched or coral-like. Formation of shallow pits, honeycomb-like compartments or short cylindrical tubes, serves the same purpose. Whereas this type of fruit is an open structure, a closed structure, in which the basidial portion is enclosed, is also found. In such sporophores the surrounding membrane is known as a **peridium** and the basidia-forming portion as the **gleba**. Forms are also known in which the gleba is at first enclosed within a tuber-like subterranean structure which at maturity ruptures and exposes the hymenium.

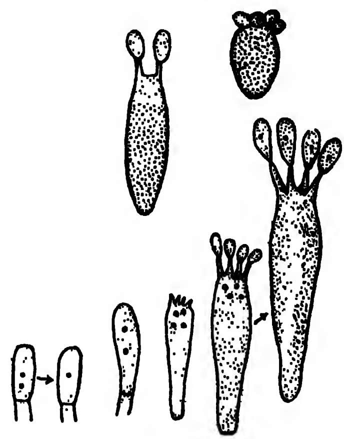


FIG. 107.—Stages in the formation of basidiospores: above, a basidium forming two basidiospores and another forming sessile basidiospores.

Many of the Eubasidiomycetes form oidia, which are uninucleate asexual spores. Their function as diploidizing agents has already been discussed.

The sub-class is divided into seven orders. Representatives of the genera *Psalliota*, *Ganoderma* and *Pellicularia* are described below.

THE FIELD MUSHROOM

The field mushroom, *Psalliota campestris* L. ex Fries, is to most people the best known of all fungi, and it is the most highly organized

fungus in the Eumycetes (Fig. 108). What is commonly called the mushroom is really the fructification, for the mycelium is not very conspicuous and remains hidden in the soil. The mushroom 'spawn', used in growing the fungus, consists of a block of richly manured soil which is permeated with it. The mycelium is septate, richly branched and dikaryotic, traversing the substratum in every direction. The mature fructification has a thick stalk, the **stipe,** swollen at the base and supporting a hat-like expansion, the cap or the **pileus.** On the underside of the pileus is an immense number of radiating gills or lamellae which are pink when young and purplish-black when mature (Fig. 16). The mycelium within the stipe is closely packed towards the outside, forming an apparently parenchymatous cortex, but towards the middle the hyphae are more loosely arranged. A little more than half-way up on the stipe is a ring known as an **annulus.** It is formed out of the remains of the **velum,** a membranous layer which covered the lower surface of the pileus at an earlier stage. The tissues of the pileus are denser, and the **gills** on the under surface are formed by their extension. These gills have a middle part formed of hyphae with a longitudinal course known as a **trama.** Towards the free surface, the mycelium has more closely packed cells forming the sub-hymenial layer, and beyond this is the hymenium itself. The hymenium consists of a palisade-like layer of club-shaped basidia which are of a somewhat stouter build. At the free end of the basidia two or four sterigmata are formed, each of which enlarges at the tip to form a basidiospore. The spores are pink when young and purplish-black when mature. The wild mushrooms have usually four basidiospores, but the cultivated ones have only two.

FIG. 108.—*Agaricus campestris*, the field mushroom, as it occurs in nature.

Mushrooms develop best in darkness, and are often cultivated in dark cellars or caves. The stipe of the mushroom is negatively geotropic, whereas the gills are positively geotropic.

Several members of the family to which *Psalliota* belongs are, however, poisonous, and one should be very cautious about eating any that have been gathered by inexperienced people. Poisonous mushrooms, known as **toadstools**, often appear in beds of edible mushrooms, and must be weeded out.

Pink Disease of Oranges (*Citrus aurantium* L.)

The disease known as pink disease is not restricted to any single host, but is widespread among plantation crops such as rubber, tea, coffee, cinchona, mango, etc., and is common all over the tropics. The fungus causing it was formerly known as *Corticium salmonicolor* Berk. & Br., but it has recently been renamed *Pellicularia salmonicolor* (Berk. & Br.) Dastur. In the Central Provinces it affects orange trees, and in some districts has become a serious threat to the further expansion of orange orchards.

The fungus is most active in the wet season, and its presence on the trees is readily noticed when the leaves wilt, turn yellow and are shed. If a diseased branch is examined, it will be found that the affected part is either covered with a fine, silvery-white film or is studded with white or pink pustules of the size of a pin's head (Fig. 109, *1*). Sometimes the affected part may be covered with pinkish pock-marks caused by the flaking off of the scales of the bark. This part of the branch, therefore, has also a pinkish appearance. In the case of thin branches and twigs, the bark, when badly diseased, is in shreds and the wood is exposed. As the disease progresses there is a shredding and exfoliating of the bark together with gumming and development of cankers.

The mycelium is at first silvery-white, with feathery or cottony margins, but at a later stage the colour changes to a general pink except at the margins, which continue to remain feathery and white. The mycelium is hyaline, thin-walled, and sparsely septate, and the hyphae may be from 7 to 15 μ broad. The pustules are white, pink, orange-red or rose-coloured. The white pustules are more or less superficial, but the coloured ones are wholly or partly embedded in the host tissues.

Another type of pustular stage is also known to which the name, the *necator* stage, has been given (Fig. 109, *4*). The pustules of the *necator* stage are in vertically elongated streaks and generally orange-red. They have a superficial resemblance to pycnidia, but their method of development is entirely different. Asexual spores

are formed on the *necator* pustules and are collectively pink but individually hyaline, thin-walled, angular or roundish, and 8–20 μ long and 5–10 μ broad. They readily germinate in water (Fig. 109, *5*, *6*).

FIG. 109.—Pink disease, *Pellicularia salmonicolor*: *1* twig with incrustation; *2* section of sporophore showing hymenium; *3* germinating basidiospores; *4* *necator* stage; *5* *necator* spores; *6* *necator* spores germinating (*1* after Butler; *2* and *3* after Zimmermann; *4* to *6* after Brooks and Sharples).

The basidial form of the fungus is rather rare, but when a hymenium is formed it is resupinate in character with broad, unseptate, club-shaped basidia. Basidia may be arranged in rows or irregularly scattered, and intermingled with them are numerous septate,

branched or unbranched paraphyses (Fig. 109, *2*). Basidia are 17–33 μ long and 5–8 μ broad, but sterigmata or basidiospores have not been observed in citrus. In rubber the *Pellicularia* stage is formed of a loose basal layer of interwoven hyphae with a dense mass of parallel basidia at the surface. The basidia give rise to four basidiospores on narrow sterigmata which may be 4–6 μ long. The basidiospores are hyaline and pear-shaped, and measure 9–12 by 6–7 μ.

The disease is disseminated by the infective material, chiefly the spores of the *necator* form, in the wet season. It persists from season to season as dormant mycelium in the callus formed round the cankers or in forks or bark tissues.

Spraying as a prophylactic measure in the case of a fungus like *Pellicularia salmonicolor*, which develops cellular aggregates inside the plant tissues, where they are well protected by suberized tissue, would not be very effective in the control of the disease. Control can best be obtained by going over the trees carefully during the dry season and examining them for the presence of cankers. These should be carefully scraped and the wound dressed with Bordeaux paste or creosote oil. As the fungus may also be found in the forks of the trees, especially those formed by the main branches, these should also be scraped and dressed with the same fungicide. In the wet season affected limbs should be cut back as soon as the disease is noticed, and to ensure complete destruction of the parasite they should be dressed as before with Bordeaux paste or creosote oil.

Several other species of *Pellicularia*—namely, *P. koleroga* Cooke, *P. filamentosa* (Pat.) Rogers (formerly known as *Corticium solani* (Prill. & Del.) Bourd. & Galz.), *P. vaga* (Berk. & Curt.) Rogers, etc. —cause disease in several plants of economic importance. *P. koleroga* causes the koleroga (rot-disease) of coffee in southern India, while *P. filamentosa* affects potatoes, chillies and other crops; its *Rhizoctonia* stage (known as *R. solani* Kuehn) is a well-known parasite of the seed-beds and of cotton, in which it causes a troublesome root-rot.

REFERENCES

AJREKAR, S. L., and LIKHITE, V. N., "Observations on *Tolyposporium penicillariae* Bref. (the bajri smut fungus)," *Curr. Sci.*, **1**, 215 (1933).

ALLEN, R. F., "A cytological study of heterothallism in *Puccinia graminis*," *J. Agric. Res.*, **40**, 585–614 (1930); **47**, 1–16 (1933).

ALLEN, R. F., "A cytological study of heterothallism in *Puccinia triticina*," *J. Agric. Res.*, **44**, 734–754 (1932).
ALLEN, R. F., "A cytological study of heterothallism in flax rust," *J. Agric. Res.*, **49**, 763–791 (1934).
ARTHUR, J. C., *The Plant Rusts* (*Uredinales*), 446 pp., 180 illus. John Wiley & Sons, New York (1929).
BRODIE, H. J., "The occurrence and function of oidia in the Hymenomycetes," *Amer. J. Bot.*, **23**, 309–327 (1936).
BULLER, A. H. R., "The diploid cell and the diploidization process in plants and animals, with special reference to the higher fungi," *Bot. Rev.*, **7**, 335–431 (1941).
CHOWDHURY, S., "Mode of transmission of the bunt of rice," *Curr. Sci.*, **15**, 111 (1946).
CRAIGIE, J. H., "Experiments on sex in rust fungi," *Nature*, **120**, 116–117 (1927).
CRAIGIE, J. H., "Discovery of the function of the pycnia of the rust fungi," *Nature*, **120**, 765–767 (1927).
CRAIGIE, J. H., "Heterothallism in rust fungi and its significance," *Trans. Roy. Soc. Canada*, 3rd ser., Sect. v, **36**, 19–39 (1942).
DASTUR, J. F., "Pink disease of orange trees in the Central Provinces," *Indian J. Agric. Sci.*, **11**, 892–901 (1941).
HANNA, W. F., "Physiologic forms of loose smut of wheat," *Canadian J. Res. C*, **15**, 141–153 (1937).
LUTHRA, J. C., and SATTAR, A., "Some experiments on the control of loose smut of *Ustilago tritici* (Pers.) Jensen, of wheat," *Indian J. Agric. Sci.*, **4**, 177–199 (1934).
MEHTA, K. C., "Annual recurrence of rusts on wheat and barley in the plains of India," *Indian J. Agric. Sci.*, **1**, 297–301 (1931).
MEHTA, K. C., "Rusts of wheat and barley in India," *Indian J. Agric. Sci.*, **3**, 939–966 (1933).
MITRA, M., "Stinking smut (bunt) of wheat, with special reference to *Tilletia indica* Mitra, *Indian J. Agric. Sci.*, **5**, 51–74 (1935).
MITRA, M., "Studies on the stinking smut or bunt of wheat in India," *Indian J. Agric. Sci.*, **7**, 459–478 (1937).
MUNDKUR, B. B., "Taxonomy of the sugar-cane smuts," *Kew Bull.*, No. 10, 525–533 (1939).
MUNDKUR, B. B., "Karnal bunt, an air-borne disease," *Curr. Sci.*, **12**, 230–231 (1943).
MUNDKUR, B. B., "Studies in Indian cereal smuts. VIII. Nomenclature of Indian smut fungi and probable mode of their transmission," *Indian J. Agric. Sci.*, **15**, 108–110 (1945).
MUNDKUR, B. B., and PAL, B. P., "Studies in Indian cereal smuts. II. Varietal resistance of Indian and other wheats to loose smut," *Indian J. Agric. Sci.*, **11**, 675–686 (1941).
PAL, B. P., and MUNDKUR, B. B., "Studies in Indian cereal smuts. I. Cereal smuts and their control by the development of resistant varieties," *Proc. Indian Acad. Sci.*, **9**, 267–270 (1939).
PRASADA, R., "Aecidial stage of rust of linseed," *Curr. Sci.*, **9**, 320–329 (1940).
UPPAL, B. N., and DESAI, M. K., "Effectiveness of dust fungicides in controlling grain smut of jowar," *Agric. Live-stock*, **1**, 396–413 (1931).

CHAPTER IX

FUNGI IMPERFECTI

UNDER the name of **Fungi Imperfecti** are gathered all those forms in which sexual stages are unknown and which are, so far as has been ascertained, merely stages in the growth and development of the Ascomycetes and a few Basidiomycetes. They are also called **Deuteromycetes** because of their imperfectly known life-cycles.

In the Phycomycetes the mycelium is coenocytic, and the asexual spores have distinctive features with whose aid it is possible to assign a fungus to a family or a genus of the class, even if the oospores or zygospores are uuknown. For instance, the oosporic stage of *Sclerospora philippensis* is unknown, but the fungus is correctly placed in the genus *Sclerospora* of the family Peronosporaceae. Similarly the perfect states of several species of *Phytophthora* and *Mucor* are unknown, but no difficulty is experienced in the classification of the species into their respective orders.

In the Uredinales a large number of imperfect forms occur, but the characteristic features of the sori are so distinctive that they are placed in the order without any hesitation. The genera *Aecidium*, *Uredo*, *Peridermium* have been established for the temporary accommodation of those species whose telial stages are unknown, but as soon as they are discovered, those species are transferred to the right genus. A rust on *Coix lachrymajobi*, for example, was known only in the uredial stage and was placed in *Uredo* and named *Uredo operta*. Recently the telial stage has been discovered and the rust re-named *Puccinia operta*. Such transfers are common in rusts. However, even though these genera are imperfect, they are not placed in the Fungi Imperfecti but are retained in the Uredinales.

As *Aspergilli*, *Penicillia* and yeasts have also a characteristic asexual fructification, they are placed in the Ascomycetes, even if their perithecial stages are unknown. In all other cases, however, fungi whose perfect states are unknown are placed among the Fungi Imperfecti.

Most of the members of this class are haplonts. Their mycelium is septate and highly branched, and reproduction is chiefly by conidia. Their classification is based on the mode of occurrence of

the conidia on the conidiophores and on their colour, shape and septation. The size of the spore is the ultimate diagnostic character for the division of the species within the genus. In practice, however, species have often been distinguished because they assume specificity to particular hosts.

Sometimes imperfecti fungi have been induced to form their perfect states by growing them on special media and in other ways. An imperfect fungus and its perfect state may bear different names because these were given before the genetic relationship between them was proved. The fungus causing the scab of apples was named *Fusicladium dendriticum* before it was known to be the imperfect state of *Venturia inaequalis*. *Colletotrichum falcatum*, which causes the red-rot of sugar-cane, has only recently been proved to be the imperfect state of *Physalospora tucumanensis*. That does not mean that all species of *Colletotrichum* have their perfect states in the genus *Physalospora*, for the perfect state of *Colletotrichum gloeosporioides*, for example, is *Glomerella cingulata* and not a species of *Physalospora*. The imperfect states of species of *Physalospora*, on the other hand, are not necessarily species of *Colletotrichum*, a genus of the Melanconiales, for the imperfect state of *Physalospora mutila*, for example, is *Sphaeropsis malorum*, a genus of the Sphaeropsidales. The perfect state of *Sclerotium rolfsii*, one of the Mycelia Sterilia, is *Corticium rolfsii*, a Basidiomycete, but on the contrary the perfect state of *Sclerotium oryzae* is *Leptosphaeria salvinii*, an Ascomycete. It is not possible, therefore, to make generalizations about the perfect states of Fungi Imperfecti.

The class is divided into three orders; a few species that cannot be accommodated in any of these orders, for they do not have even the conidial fructifications, are placed in the Mycelia Sterilia.

Conidiophores superficial on a simple mycelial branch or united into bundles or strands or forming cushions of matted hyphae or of stromatic pseudoparenchyma	**Moniliales**
Conidia borne in pycnidia or chambered cavities and set in the substratum	**Sphaeropsidales**
Conidia borne in definite acervuli and finally free in the substratum	**Melanconiales**
Spores unknown	**Mycelia Sterilia**

There are six families in the Moniliales, four in the Sphaeropsidales, and one in the Melanconiales. These families are not based on phylogenetic relationships but on superficial and artificial resemb-

lances. The genera comprising them are therefore known as **form-genera**. As an aid in identification, the families are divided into sections depending on their spore characters as follows:

Spores one-celled, round or egg-shaped, elongate.	**Amerosporae**
Hyaline or bright	*Hyalosporae*
Dark or swarthy	*Phaeosporae*
Spores two-celled, egg-shaped or elongate . .	**Dimerosporae**
Hyaline or bright	*Hyalodidymae*
Dark or swarthy	*Phaeodidymae*
Spores three- or more-celled, oblong to fusoid .	**Phragmosporae**
Hyaline or bright	*Hyalophragmae*
Dark or swarthy	*Phaeophragmiae*
Spores muriform, ovate or elongate	**Dictyosporae**
Hyaline or bright	*Hyalodictyae*
Dark or swarthy	*Phaeodictyae*
Spores acicular to filiform, or worm-shaped, one- to many-celled	**Scolecosporae**
Spores cylindric, spirally twisted, one- or more-celled	**Helicosporae**
Spores stellate, one- to many-celled	**Staurosporae**

MONILIALES

Moniliales, also known as **Hyphomycetes**, have a septate mycelium which is branched, and hyaline or dark-coloured. Reproduction is solely by means of conidia, which are produced in the most varied manner on the conidiophores or their branches. Conidia have many different shapes and colours. Conidiophores may be short, upright branches or bound into coremia or in layer-like bolsters. Some of the more important genera whose members cause disease in plants are *Alternaria*, *Fusarium*, *Cercospora*, *Helminthosporium* and *Piricularia*. Diseases caused by some of them are described below.

Early Blight of Potatoes (*Solanum tuberosum* L.)

Early blight of potatoes caused by *Alternaria solani* (Ell. & Mart.) Jones & Grout is of widespread occurrence in India and abroad, and appears, as a rule, three to four weeks after the crop is sown. In the Indian plains, where late blight (which appears three to four weeks after early blight) is rare, early blight is the most destructive fungal disease.

The disease first becomes visible when small, isolated, pale-brown spots appear on the leaves. They are scattered irregularly, and under certain conditions they remain small and more or less

angular, being limited by the veins. The number of spots may be few, but when the disease appears in a severe form a large part of the leaf-surface is involved. As they grow in size they become irregularly circular and usually show a series of concentric ridges which produce a 'target board' effect (Fig. 110, *1*). There is often a narrow marginal faded zone which spreads out as the spot enlarges. The spots increase in size after the death of the leaf.

Potato plants may suffer from early blight at almost any stage, but under ordinary conditions the disease is not able to gain a foothold until the plants have passed their period of greatest vigour.

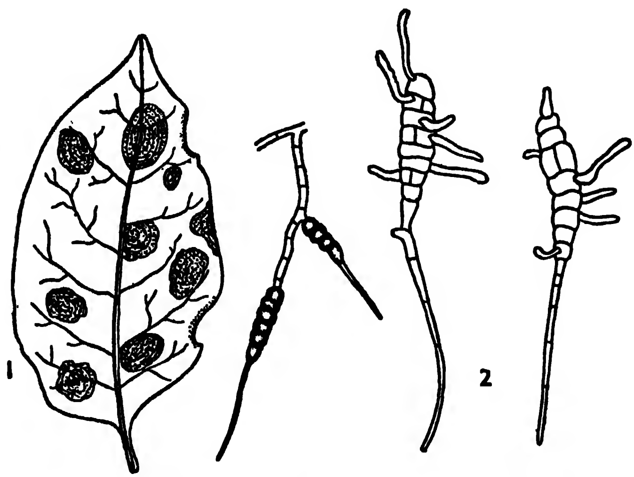


FIG. 110.—Early blight of potatoes, *Alternaria solani* : *1* affected leaf; *2* spores.

The effect of the disease on the crop is considerable. If conditions are favourable, the spots increase in number, and the leaves, beginning with the lower ones, gradually die until only a few remain at the top. In severe cases spots may develop on petioles and stems.

The mycelium consists of light-brown, slender, radiating, sparsely branched filaments ramifying in the intercellular spaces and also penetrating the cells of the invaded tissues. Later it becomes closely branched, irregular and deeply stained. Conidiophores emerge through the stomata from the dead centre of the spots and are 50–90 μ long and 9 μ broad. Conidia are borne singly and arise on the conidiophore, not by constriction and subsequent enlargement of a terminal cell, but from a bud which forms on that cell. Conidia are variable in shape, mostly obclavate, terminating in a long, septate

and sometimes branched beak. There are five to ten septa and there may be longitudinal septa also (Fig. 110, *2*). The conidia measure 130–300 μ in length and 12–20 μ in breadth. In moist weather spores germinate readily and five to ten germ-tubes may arise from a single conidium. Infection as a rule is through the stomata, but direct penetration through the epidermal walls may also, though rarely, take place. The incubation period varies from forty-eight to seventy-two hours.

Climate and soil exert a controlling influence upon the development of the disease. It becomes serious when the season begins with abundant moisture followed by high temperatures unfavourable to the host plant. Periods of continued drought check its spread. Crop rotation is a rational measure to avoid primary infection from spores that have over-wintered or over-summered in the soil. Dead haulms should be raked together and burned immediately after harvest. Timely and thorough spraying with Bordeaux mixture effectively controls early blight. Weekly spraying must be given from the time the plants are 6–8 inches high and continued throughout the period of their growth.

Tikka Disease of Ground-Nut (*Arachis hypogea* L.)

A serious leaf-spotting and defoliation of ground-nut plants is rather common in many areas where this crop is grown in India. At one time it was believed that the disease was due to a single fungus; but it has recently become increasingly manifest that there are two leaf-spots, one due to *Cercospora personata* (Berk. & Curt.) Ell. & Ever., and the other to *Cercospora arachidicola* Hori. The symptoms produced by these two different species of *Cercospora* are strikingly different. In India the former appears to be more widespread and causes greater damage than the latter.

All parts of the plant above the soil-level are attacked by both the fungi, and the early symptoms are not clearly distinguishable. But very soon marked changes occur in the symptoms they produce, and it is then comparatively easy to say which is due to *Cercospora personata* and which to *Cercospora arachidicola*. The leaf-spots produced by the former are more circular, 1–6 mm. in diameter, and the necrotic lesions on both the surfaces very early assume a dark-brown to almost dark colour (Fig. 111, *1*). There are no halos around the young spots, but bright yellow halos develop around the more mature ones on the upper surface. The mycelium is entirely

internal and strictly intercellular, and branched haustoria develop in the palisade and spongy mesophyll cells. At the time of conidial production the identification of the disease becomes unmistakable. Conidiophores of *Cercospora personata* are 24–54 μ long and 5–8 μ

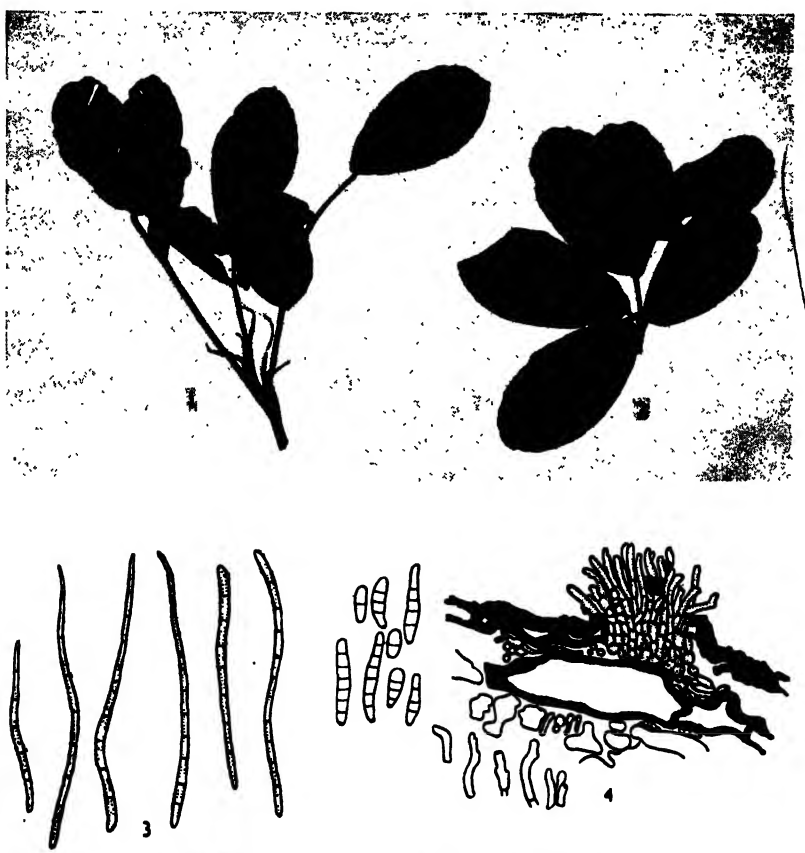


FIG. 111.—Tikka disease of ground nut: *1* symptoms due to *Cercospora personata*; *2* symptoms due to *Cercospora arachidicola*; *3* conidia of *Cercospora arachidicola*; *4* conidiophores and conidia of *Cercospora personata.*

broad, continuous or 1- to 2-septate and geniculate (shouldered), the points at which conidia were attached being clearly visible. They emerge by rupturing the epidermis in tufts, their base being densely stromatic. Conidia are obclavate or cylindrical, measure 18–60 μ in length and 6–11 μ in breadth, and are 1- to 7-septate (Fig. 111, *4*).

Leaf-spots caused by *Cercospora arachidicola*, on the contrary, are

irregularly circular, often confluent and larger in size, varying from 4–10 mm. in diameter (Fig. 111, *2*). A circular, bright yellow halo which blends into the green of the leaf is manifest from the very beginning. The halos are much less distinct on the lower surface of the leaves. The mycelium is both internal and external, intercellular and intracellular, but it is without haustoria. Conidiophores are amphigenous, but on the younger spots they are produced exclusively on the upper surface. They are yellowish-brown, and as conidia are formed and abjointed apically, they continue to grow past them and become geniculate. Conidia leave definite scars as they fall away. Conidiophores are 22–41 μ long and 3–5 μ broad, continuous or 1- to 2-septate. Conidia are hyaline or pale yellow to slightly olivaceous, obclavate, 38–108 μ long and 3–6 μ broad. They are 4- to 12-septate (Fig. 111, *3*).

The perfect states of both these species have been found on fallen leaves and stems late in autumn or in early winter in the United States. The perfect state of *Cercospora personata* is named *Mycosphaerella berkeleyii* W. A. Jenkins, and that of *Cercospora arachidicola*, *Mycosphaerella arachidicola* W. A. Jenkins.

Both the diseases are disseminated by wind which blows the spores from leaf to leaf. Attacks in the new crop are apparently initiated by the spores which lie in the soil. There is evidence to show that they are seed-borne, especially in the shells. Seed treatments have given clean crops, indicating that seed infection cannot entirely be ruled out. If the precise phenological relations of the disease are determined and the time of appearance noted, then spray schedules can be made. Bordeaux mixture appears to have given quite good results. Foliage, however, must be thoroughly covered by the protective layer both on the upper and lower surfaces.

Beneficial results have also been obtained by good cultivation and proper rotations. Some of the early maturing exotic varieties are reported to have shown considerable resistance to the disease.

Wilt of Pigeon Peas (*Cajanus cajan* (L.) Millsp.)

A wilt of pigeon peas caused by *Fusarium udum* Butler occurs wherever this crop is grown in India. Precise estimates of the actual losses that are caused are not available, but reports received from the provinces indicate that it is especially destructive in parts of Bombay, the Central Provinces, the United Provinces and Bihar. No other disease does more damage to pigeon peas than wilt does, and

it has therefore attracted great attention from very early times. The disease becomes manifest in the crop when the plants are about five to six weeks old, at which time the leaves of the attacked plants turn prematurely yellow and wither, until finally the entire

FIG. 112.—Wilt of pigeon peas, *Fusarium udum* (courtesy H. W. Wollenweber).

plants dry up. Death follows very soon after. As the season advances and the plants mature, the number of deaths increases, and more than 50 per cent of the plants in the field are known to succumb to the disease (Fig. 112).

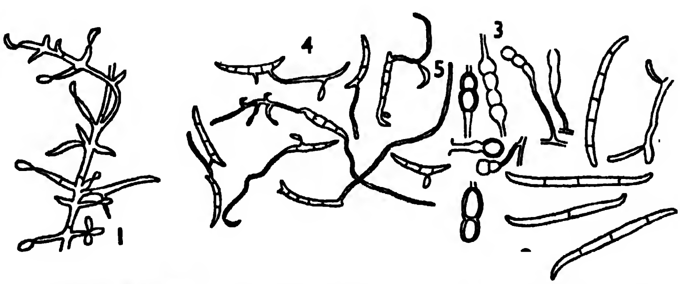


FIG. 113.—*Fusarium udum*: *1* mycelium showing microconidia; *2* macroconidia; *3* chlamydospores and their formation; *4* germination of macroconidia; *5* microconidia (after Butler).

That the death of the plants is not due to drought is evident from the fact that wilt is not uniformly spread in a field, and the soil will be found on examination to have enough moisture for the normal growth of the crop. If attacked plants are dug up and examined, it

will be found that the vascular tissues of the roots and stem are blackened in streaks which may be thin in the early stages of attack but are thick bands in later stages (Fig. 114). These black streaks can be traced up the stem to a height of several feet, and the earliest branches to wither are those which arise from such blackened parts. Wilting may sometimes be partial, as only one side gets withered; in such cases the stem is blackened on that side alone.

As a rule most of the attacked plants succumb completely to the disease, but where attack is partial, only the parts attacked dry up. Recoveries, if any, are rare, though the plants that show the symptoms of attack linger for a month or more before death overtakes them. Sudden wilting has been reported, but it is rather rare.

The fungus in an attacked plant is as a rule restricted to the vascular tissues and is both intercellular and intracellular. Hyphae run through the cells, growing with great rapidity along the inside of the walls of the larger vessels, and permeate the entire root system and the stem. The profuse growth of the mycelium within the lumen of the xylem vessels, and the consequent plugging by matted coils of hyphae, interfere with the free flow of water to the green parts of the plant, so that a drooping and wilting of the leaves results. The fungus secretes substances which are toxic to the living cells in the tissues concerned in the ascent of sap.

Infection takes place through the tender lateral roots and rootlets and possibly root-hairs, but at what precise age of the plant it occurs has not yet been determined. That it never takes place in the parts above ground is quite certain. Mycelium is hyaline and produces spores of three types within the tissues of the host plant—macroconidia, microconidia and chlamydospores (Fig. 113, *1*, *2*, *3*). Macroconidia are produced in small cushions of stromatic mycelium on the surface of the bark. They are long, curved, pointed at the ends, septate, and measure 15–50 μ in length and 3–5 μ in breadth. They are formed on short conidiophores and shed when mature, without being held together in a ball. Microconidia are small, elliptical or curved, unicellular or with one or two septa, and measure 5–15 μ in length and 2–4 μ in breadth. They are formed within the tissues and usually become free on falling, but in culture media and on the surface of the plant they are held together in a little drop of liquid at the tip of the hypha, until as many as a dozen or more are present in a drop. Chlamydospores are formed within the tissues. In their formation a spherical or oval cell rounds off and becomes

thick-walled, and several such chlamydospores may occur one below the other in a chain (Fig. 113, *3*). Chlamydospores are more durable and are capable of retaining their viability for a longtime.

Fusarium udum is a facultative parasite and can remain in the soil in a viable state for long periods of time. Its spores, both microconidia and macroconidia, remain viable for a considerable time, while the chlamydospores do so for even longer periods. When the crop is sown in soil infested by ***Fusarium udum***, the fungus attacks the plants. Wilted plants first occur in patches and spread gradually in the field, infection being carried by attacked roots to new areas. Air-borne infection through spores produced on the surface of the stems is negligible, as the parts above ground are not attacked.

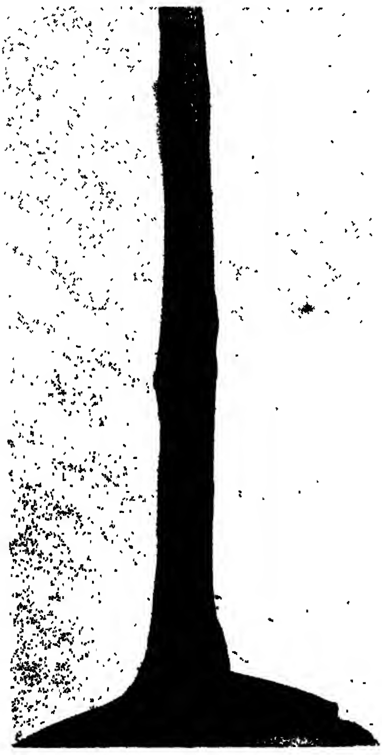


FIG. 114.—Wilt of pigeon peas; stem cut into two to show infection of vascular region by mycelium of *Fusarium udum*.

There is no direct treatment for controlling pigeon pea wilt. If long rotations are practised, the disease can be effectively reduced in intensity. Such rotations are common, and that may be the reason for the disease being not as serious as it might have been. The crop should not as a rule be sown on the same soil for two to three years in succession.

Development of resistant varieties offers the best method of control. A few such varieties with a high degree of resistance have been discovered by the Mycological Division of the Indian Agricultural Research Institute at New Delhi, but most of them have poor agronomic qualities and are not very palatable.

A wilt disease of cotton due to ***Fusarium vasinfectum*** Atk. occurs

in several parts of India, especially the Bombay and Central Provinces and Central India. The disease is restricted to the black cotton soils, which are heavy clays with an alkaline reaction, but in the light alkaline and loamy soils it is unknown. The fungus enters the host when the plants are one to three weeks old, and the symptoms produced in the cotton plants are similar to those produced in pigeon peas attacked by *Fusarium udum*. They become manifest when the plants are five to six weeks old and, while complete death is the rule, partially attacked plants are not uncommon. Like pigeon pea wilt, this disease cannot be controlled by direct means, but resistant varieties that have the desired agronomic and commercial characters have been developed by the Bombay Department of Agriculture and have replaced the old susceptible varieties; cotton wilt is thus to a large extent under control. In India all the New World cottons are immune to wilt, even those that are highly susceptible to the disease in the countries from which they have been imported, for example, the United States. Wilt occurs in that country in sandy acidic soils, and when those American varieties are grown in the heavy clayey and alkaline soils of India, they apparently acquire complete immunity to the disease. When the susceptible Indian varieties are grown in the sandy acidic soils in the United States it is noted that they also acquire immunity to the disease, indicating that the reaction and texture, among other factors, play an important rôle in rendering plants susceptible or resistant to disease.

Helminthosporium Disease of Rice (*Helminthosporium oryzae* L.)

Helminthosporium leaf-spot of rice due to *Helminthosporium oryzae* Brede de Haan is a widely distributed disease throughout south-eastern Asia, Japan, the Philippines, and to a smaller extent in the southern states of the United States. Within India the disease occurs in an epiphytotic form in Assam, Bengal, parts of the Madras province and Sind. It is relatively less important in the other parts of the country.

The fungus attacks all parts of the plant in all stages of development. In the seedling stage the plants are attacked when they are 2–3 cm. high. The tips of the cotyledons become brown or dark brown and the infection spreads to the hypocotyl, which thus gets weakened and the seedlings succumb to the disease. Spots on the foliage are very common and form the first conspicuous symptom (Fig. 115). They appear in the form of small pinhead-like brown

areas on both the surfaces, a larger number being discernible on the lower surface. They gradually increase in size, and become dark brown with a yellowish halo surrounding them. The number rapidly increases, and up to 300 spots may be seen on a single leaf. Later they coalesce and become irregular in shape. The central part of the spots take on a greyish discoloration, and the entire leaves

FIG. 115.—*Helminthosporium* disease of rice; infected leaves and ears.

may also become greyish-brown and finally perish. When the attacks are severe the heads are unable to emerge from the sheaths and perish without developing fully. Where heads have emerged they are distorted in various ways. Culms are also affected, and blighted culms turn yellow, then pale brown and finally dark brown; their surface is covered with the conidiophores, which give them a velvety appearance. Lesions on the heads first appear on or near the lowest joints of the rachis, and these neck lesions are somewhat

similar to the 'rotten neck' caused by *Piricularia oryzae*. Infection of the glumes first appears near the joint of the outer and inner glumes, and lesions gradually spread over the whole surface. When the disease is severe there may be no grain formation and the ears may become sterile (Fig. 115).

The fungus is both intercellular and intracellular. Conidiophores (Fig. 116) are stout, erect and arise in tufts through the stomata and rarely through the ruptured epidermis. They are dark-olive nearer the base and paler towards the tip, and unbranched except at the base, where they sometimes form branches. They are bent and have knee-like projections where conidia are borne. The lowest conidium is the oldest. Conidiophores may be up to 680 μ long, but in India it has been found that they are never longer than 175 μ and 5–7 μ in breadth. Conidia are 5- to 10-septate; their smallest mean length is 56 μ and the largest 104 μ, and the smallest mean width is 15 μ and the largest 20 μ (Fig. 116).

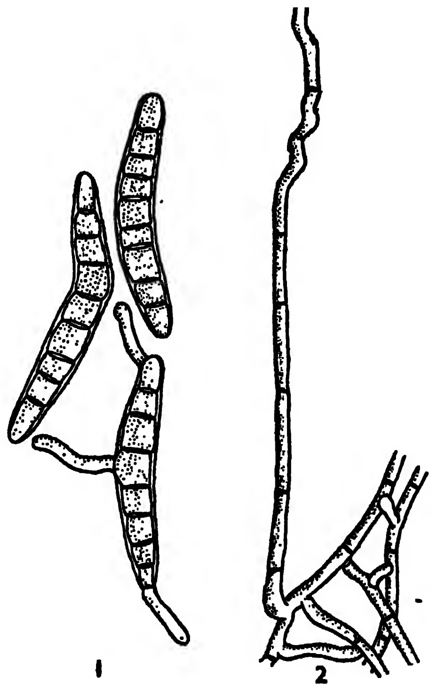


FIG. 116.—*Helminthosporium oryzae*: *1* conidia; *2* conidiophores (after Drechsler).

Heavy and continuous rains with days of cloudy weather are favourable for the development and spread of the parasite. The disease is also very common in tracts where rice is grown under irrigation. In Bengal it occurs both on the kharif and the rabbi crop, but it has been observed that it is more common in the latter crop.

Attempts at the direct control of the disease have not so far given very encouraging results. It is both internally and externally seed-borne, and while seed treatments reduce the severity of infection, they cannot eliminate internal infection. Hot-water treatment has

been tried in Japan and other countries, but the details of its application are not precisely known. Varieties of rice have not shown any remarkable degree of variation in their susceptibility or resistance to the disease, but a more intense search for resistant varieties is likely to prove successful.

SPHAEROPSIDALES

Sphaeropsidales, also known as Phomales or Phyllostictales, have a septate mycelium which is profusely branched. Conidia are formed in pycnidia, which are the most characteristic feature of the order. Pycnidia are with or without ostioles and separate or joined by stromatic tissue. Pycnidiospores are slime-spores, hyaline or coloured, septate or unseptate. All members of this order, so far as at present known, belong to the various families of Ascomycetes. The more important genera whose members cause destructive plant diseases are *Ascochyta*, *Diplodia*, *Macrophomina*, *Phyllosticta*, *Phomopsis* and *Septoria*.

Blight of Gram (*Cicer arietinum* L.)

A serious blight of gram caused by *Ascochyta rabiei* (Pass.) Labrousse is very common in certain parts of the Punjab and the North-West Frontier Province. It very frequently appears in an epidemic form, and a loss of up to 50 per cent of the crop has sometimes been reported.

The fungus attacks all the above-ground parts of the plant, and circular spots appear on the leaves and pods, and elongated ones on the petioles and stems (Fig. 117, *1* and *2*). When the spots on the stems girdle them completely the parts above the lesion droop and get dried. On the leaves the spots gradually spread and coalesce, and the entire leaf turns brown and has a scorched appearance. If the spots at the base of the plants girdle the stem, the entire plants wither and finally die. As the disease advances, patches of diseased plants become prominent in the field and slowly spread, involving the entire field.

If the weather during this period is dry the disease remains restricted, but if there is rain at the time and the whole crop is involved it may be completely destroyed in a few days.

The mycelium of the fungus is hyaline to brownish and septate. Pycnidia appear as minute, blackish dots in concentric zones on the spots and give them a characteristic appearance. They are spherical

to pear-shaped, with a prominent ostiole. Conidia are borne on short conidiophores within the pycnidia and lie embedded in a slimy material (Fig. 117, *3*). If the pycnidia are moistened, they absorb water, swell, and a slimy mass oozes out, together with the conidia,

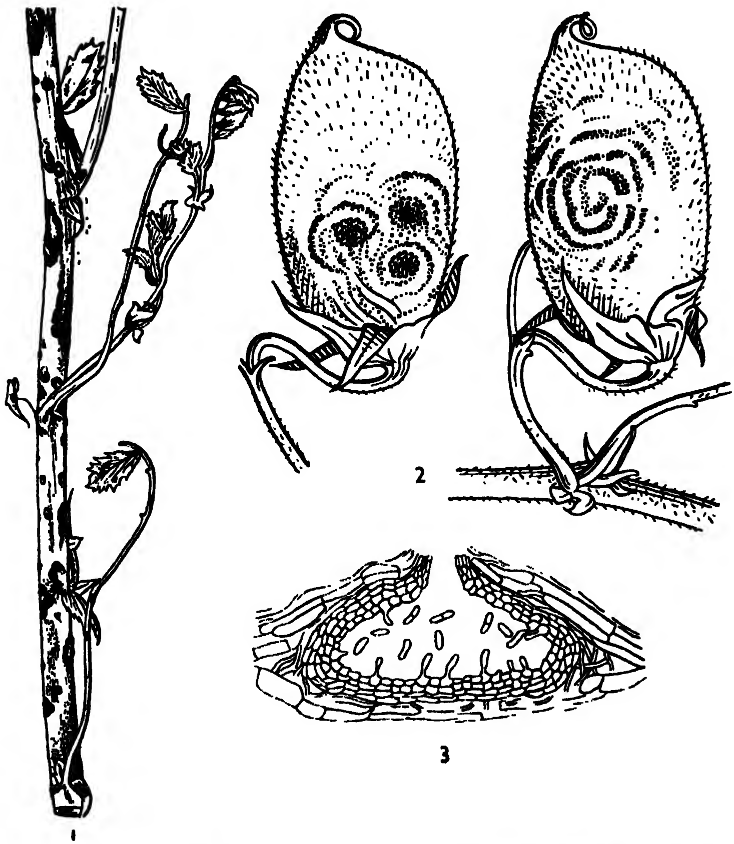


FIG. 117.—Blight of gram, *Ascochyta rabiei* : *1* affected plant showing lesions; *2* affected pods; *3* pycnidium showing conidiophores and conidia (after Butler).

forming long spore-horns. The spores are oval to oblong and 10 μ long and 4 μ broad. They are mostly one-celled, but a few, up to 5 per cent, may be two-celled. They germinate by forming long germ-tubes as soon as they are mature. Experiments conducted at Lyallpur have shown that they remain viable within the pycnidia for

considerable periods of time, up to a year or more. The perfect state of the fungus on the fallen leaves and stems has been discovered in Bulgaria and named *Mycosphaerella rabiei* Kovachevsky.

The disease is both externally and internally seed-borne. Within the seed it may be in the form of mycelium or as pycnidia, and seed treatments with fungicides are not of much use, though they may reduce the quantity of inoculum. Hot-water treatment is likely to prove useful in eliminating the internal infection, but does not appear to have been given a trial. Both in the Punjab and the North-West Frontier Province there are areas where blight is practically absent and where it is possible to obtain infection-free seed. The use of such seed has been of much help in reducing losses. Plant debris left lying in the fields after the crop is harvested is also a source of infection capable of initiating epidemics in the following year. Ploughing the fields with a furrow-turning plough after the first summer shower, in order to bury the remnants of diseased plants, has given much relief. Blighted plants must be pulled out by hand and burned, if possible. These measures help considerably in eliminating the over-summering inoculum and in reducing the severity of epidemics. Spraying with Bordeaux mixture is not a practical proposition, as the area to be covered is vast and the cost may be prohibitive.

Some years ago the Punjab Department of Agriculture secured varieties of gram from all over India and several countries abroad. One or two varieties obtained from the United States proved highly resistant to blight. These varieties compare very well in their agronomic and other characters with the local ones, and have almost replaced the older susceptible varieties. As a result of these efforts, gram blight is to a large extent under control.

Stem-Canker of Pigeon Peas (*Cajanus cajan* (L.) Millsp.)

A stem canker of pigeon peas, especially at the collar region, due to *Diplodia cajani* Raychaudhuri is becoming increasingly common in Bihar and the United Provinces and appears to be spreading. It is apparently widespread in Puerto Rico and the West Indies, especially Trinidad. The disease appears when the plants are two to three months old, in the form of small, grey, scutiform lesions with dark edges, on the stems, branches and twigs. The lesions when fully developed are up to 5 cm. in length, and are more common at the collar region. They turn into large, deep-seated

cankers with a markedly verrucose and carbonaceous surface. Outside the limits of the lesions, callus is usually formed, and because of the unequal development of the woody tissues in the region of the lesions a twisting and distortion of the stems take place. The tissues of the stems near the canker are discoloured to a height of several feet, but this discoloration does not extend to the roots. Cankers formed at the collar girdle the stem, bringing about the sudden wilting and death of the plants. Where the cankers have not girdled the stem they coalesce if there are several of them near each other, and render the plants so weak that any strong breeze will break them.

The mycelium of *Diplodia cajani* is septate and hyaline, though in the old cankers it may be slightly olive-brown. It is 3–8 μ in breadth and is usually intercellular. Pycnidia are simple, globose, osteolate, and at first immersed, but later burst through the epidermis. Conidia are borne on short, needle-shaped pedicels, and though they are at first hyaline, they turn dark brown and two-celled. They are oval, and their average length is 25 μ and breadth 13 μ.

Detailed investigations on the mode of transmission, perpetuation and method of infection of the host by the parasite have yet to be made, but the fungus appears to gain entry through injuries to the stems caused by cultural operations, insects, etc. Control measures have not yet been devised, but if injuries to the plant at the region of the collar are avoided, the damage can probably be minimized.

Stem-Rot of Jute (*Corchorus capsularis* L.)

Stem-rot of jute caused by *Macrophomina phaseoli* (Maubl.) Ashby is a serious disease of the crop in Assam, Bengal, Bihar and Orissa. Both the quality of the fibre and its out-turn are affected, and the losses caused when epidemics are severe are enormous. Plants in all stages of growth are attacked, and when mortality is high large gaps occur in the fields. Jute is as a rule thickly sown so as to minimize branching of the plants. The plants therefore develop tall, supple stems yielding fibre of excellent quality. But when there are gaps, stems are uneven and ret poorly, yielding a coarse, brittle fibre. Gaps moreover induce branching, rendering the plants unsuitable for fibre production, and must therefore be avoided.

On the seedlings the earliest symptoms appear on the hypocotyls and cotyledons in the form of blackish-brown streaks. In younger seedlings damping-off is common if the weather is moist, but in older ones there is a shedding of the leaves, rotting of the stems and

finally death of the plants. In mature plants necrotic lesions on the leaves appear at the apex and along their margins, but soon the entire leaf-blade, midribs and petioles are completely involved. Lesions are common on the stems as blackish-brown depressions which increase in size, and several such lesions coalesce and girdle the stem (Fig. 118). Where streaks run along the length of the stems without girdling them, the cortex becomes shredded, exposing the fibrous tissue. Root infection is rare. In severe cases capsules and seeds are also attacked, pycnidia and sclerotia being formed on them.

FIG. 118.—Stem-rot of jute, *Macrophomina phaseoli* (courtesy B. S. V. Rajan).

The mycelium penetrates all the tissues of the stem, epidermis and cortex being most affected. Pycnidia are embedded in the epidermis, but sclerotia are restricted to ray cells and softer tissues of the phloem and xylem. Sclerotia are black and spherical, and vary in diameter from 40 to 85 μ. Pycnospores measure 16–27 μ in length and 6–10 μ in breadth.

Observations made at Dacca indicate that there are two phases of the disease. During the first phase the fungus kills a large number of seedlings and young plants in the first two months. During the second phase, which starts after the plants are four to five months old, there are no deaths, but the quality of the fibre is ruined owing to the formation of cankers and shredding.

The disease is both soil- and seed-borne, but primary infection appears to be chiefly due to infected seed. As pycnidia are embedded in the tissues of the seed, external seed treatments are of little use. Use of clean seed from localities where the disease is not present is the best method to reduce primary infection and the severity of the disease. There may be varieties of jute that are resistant to attack by this fungus, but so far none has been discovered. No other method of control is known.

MELANCONIALES

A large number of species of this order are plant parasites. Their mycelium is as a rule in the interior of the host plants, and fructifications are formed in acervuli which lack a peridium. The substrate itself may, however, form a protective cover. Acervuli are usually sub-epidermal, at times remaining covered, but usually erumpent and bright-coloured to black, and surrounded by the torn edges of the covering membrane. Conidiophores stand thickly beside one another and are simple or rarely branched and hyaline or dark-coloured. Spores are formed singly or in chains. The more important genera are *Colletotrichum* and *Pestalotia*.

Red-Rot of Sugar-Cane (*Saccharum officinarum* L.)

Of all the diseases that affect sugar-cane, red rot due to *Colletotrichum falcatum* Went is easily the most serious and destructive. It is very widespread in many countries where sugar-cane is grown on a large scale, and in India it occurs in most of the Provinces and States. In north Bihar and the eastern United Provinces it appeared in such a virulent and destructive form between 1939 and 1942 that it threatened the very existence of the sugar industry.

The fungus attacks all the parts above ground, but more especially the stems and midribs of the leaves. In the stems infection is as a rule internal, and external examination may not reveal the presence of the disease. When the stems are completely rotted within, the rind loses its naturally bright colour, becomes dull in appearance and shrinks at the nodes. At about this time the upper leaves turn paler and droop slightly. They wither at the tip, and the withering process spreads down along the margins, leaving the centre green. When the disease appears in a severely epidemic form the whole crop withers and droops, and by the end of the season little or nothing may be left unaffected.

When the affected stems are split open, the tissues of the internodes, which are normally white or yellowish white, will be found to be longitudinally reddened in one or more internodes, usually towards the base. The reddening is most intense in the vascular bundles, but extends to the pith. This red colour is interrupted by white patches extending crosswise on the stems, and these are so characteristic of the disease that in their absence it may not be possible to diagnose it correctly without a microscopic examination.

Formation of red colour within the tissues is a natural reaction of sugar-cane plants to any sort of wounding, but such reaction is usually limited to the immediate borders of the injury. In the case of true red rot, the colour extends through many internodes (Fig. 119).

On the midribs, infection originates as a dark-reddish area which elongates rapidly, forming blood-red lesions with dark margins (Fig. 120, *1*). In older lesions the centre becomes straw-coloured, and when the fructifications are formed, the lesions are covered with powdery masses of conidia.

Red-rot epidemics cause heavy losses in yield and, because of the

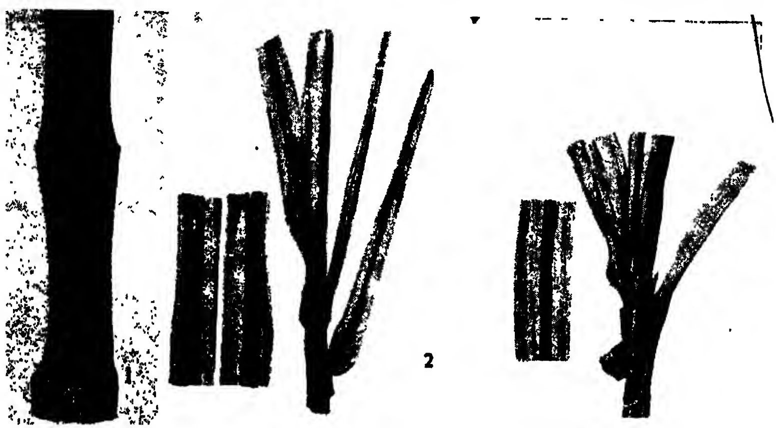


FIG. 119.—Red rot of sugar-cane showing lesions on *1* stem; *2* midribs.

inversion of sucrose, reduction in the recoverable sugar in the factory. Such losses in sucrose may be as high as 33 per cent. When the disease appears in a virulent and epidemic form, not only is the reduction in stands enormous, but entire fields have been wiped out.

The mycelium of the fungus is chiefly found in the parenchymatous cells of the pith and in spaces between them. Hyphae are slender, freely branched, colourless and septate, and contain characteristic droplets of oil. Acervuli are formed on the surface of the rind as minute clusters of black, velvety bodies, just above or below the nodes, in depressions or ridges due to shrinking of the stems. Conidiophores are unseptate and 20 μ long and 8 μ broad (Fig. 120, *3*). Conidia are one-celled, usually falcate, hyaline and densely granular, frequently guttulate, and 16–48 μ long and 4–8 μ broad (Fig. 120, *4*).

Terminal or intercalary, thick-walled, greenish-black chlamydospores are present. Long, rigid, bristle-like setae, which are septate, dark below and lighter above, are present in the stroma (Fig. 120, *2*). They are up to 200 μ long and 4 μ in diameter, and are either intermixed with the conidiophores or form a fringe around the acervulus. On germination the conidia develop a mycelium or produce appressoria (Fig. 120, *5*).

The ascigerous or perfect state of the fungus has been recently discovered in the United States both in pure culture and under

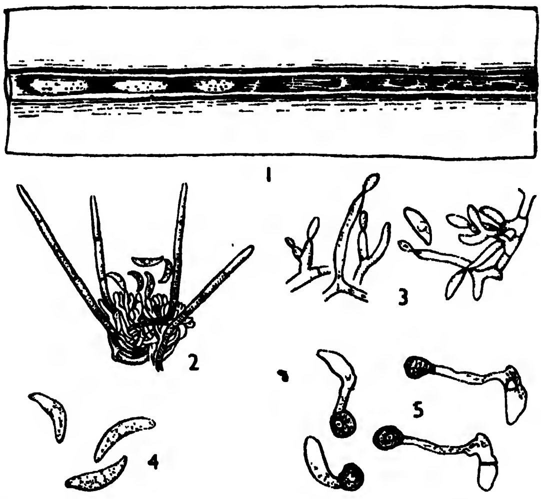


FIG. 120.—Red rot of sugar-cane, *Colletotrichum falcatum*: *1* leaf showing lesions; *2* acervulus showing setae, conidia and conidiophores; *3* conidiophores and conidia; *4* spores; *5* germination of conidia with formation of appressoria (after Butler).

certain conditions in the field. The ascigerous stage is a species of *Physalospora*, one of the Sphaeriale, and agrees best with *Physalospora tucumanensis* Spegazzini; this name was given in 1896, Spegazzini being unaware that it is the perfect state of *Colletotrichum falcatum*.

There is a considerable body of data to indicate that red rot is borne in the setts. According to a general belief among plant pathologists, the fungus is unable to persist in the soil, which is therefore relatively unimportant as a source of inoculum. It has recently been asserted in India that it may persist in the soil up to six months, but satisfactory evidence is not yet forthcoming to prove that contention. If sugar-cane trash from diseased plants is

buried in the soil, a good deal of disease appears in the crop. Such trash may therefore perpetuate the disease, but how long the fungus mycelium remains viable in it has yet to be accurately ascertained.

Secondary spread of the disease is principally by means of conidia from the midrib lesions, on which they are produced in great abundance. They enter the cane through the nodes, where numerous scars are left by the tearing-off of the leaves. The enclosing sheaths retain moisture which helps the conidia to germinate. Stem infection may be through borer tunnels, root primordia and seed-cuttings by conidia produced in the trash. Though roots are infected, red rot is not a root disease.

One of the principal methods of controlling red rot is to use sound healthy setts. If they are sown in plots where long rotations are practised, there is little likelihood of an epidemic. Reserving separate seed-plots to raise healthy setts has given good results. If such plots are properly fertilized, cultivated, and constantly rogued of all diseased plants, seed of high quality is assured. Destruction of trash and other diseased material, sound cultural practices, and avoiding covering seed setts too deeply, are excellent means of reducing infection.

The most effective method of controlling the disease is, however, the utilization of resistant varieties, and this is one of the principal aims of sugar-cane research in India. Parasitic races do not probably exist, but cultural races have been found which differ in their virulence. One such race has light-coloured mycelium with a capacity to sporulate abundantly, and a second race is dark-coloured and does not sporulate so freely and appears to be less pathogenic. Varieties which show a good deal of resistance to both these cultural races have been found, and are now replacing those that are most susceptible to red rot.

Grey Blight of Tea (*Thea sinensis* L.)

Grey blight of tea caused by *Pestalotia theae* Sawada is the commonest blight of this crop in India; it has been reported from Java, Formosa and the Caucasus regions, and is apparently co-distributed with its host. As a rule only the old bushes are attacked, the disease being at first restricted to one side of the bush. It then works round until every leaf is killed. This destruction is sometimes so severe that the bush is seriously damaged. Sometimes young shoots and stem may be affected.

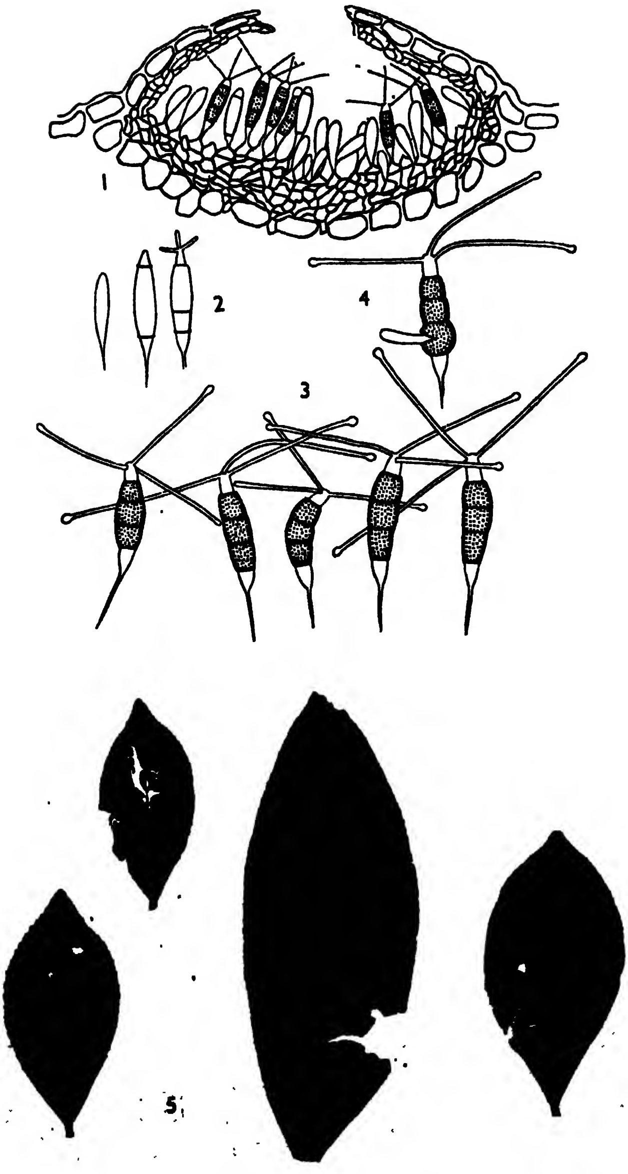


FIG. 121.—Grey blight of tea, *Pestalotia theae* : *1* section through a pycnidium; *2* stages in the development of conidia; *3* mature conidia; *4* germination of a conidium (all after Butler); *5* tea leaves showing spots due to blight.

The attack begins on the upper surface of the older leaves as minute brownish spots which soon turn grey. As the spots increase in size, they coalesce, forming patches of variable size and irregular outline, involving the greater part of the leaves. Later the spots appear on the under surface, but they do not turn grey. Narrow concentric bands of alternate lighter and deeper shades, especially near the margin, may often be seen on the upper surface (Fig. 121, *5*).

Mycelium is intercellular and sparingly septate and hyaline. Fructifications are formed within the acervuli, which are sub-epidermal. The acervuli have a basal wall which is distinct, but the lateral and apical walls are rather obscure. These structures have sometimes been classified as pycnidia rather than as acervuli, and the genus has sometimes been classified in the Sphaeropsidales (Fig. 121, *1*). The conidiophores occur on the inner wall of the lower half of the pycnidium, and conidia are formed on their tips. When ripe the conidia are detached, but the stalks remain as an appendage at the base of the conidium. The upper layer consisting of the epidermis and the slender wall of the acervulus ruptures, liberating the conidia.

Conidia are spindle-shaped, divided by four septa into a row of five cells, of which the central three are dark-coloured, while the other two form a kind of colourless cap at each end (Fig. 121, *3*). The conidiophores persist at the lower ends of the conidia, but from the opposite end, the end cells grow out into three, or rarely four, colourless, thread-like appendages of considerable length, which aid in securing the dissemination of the conidia. Conidia measure 22–33 μ in length and 6–7 μ in breadth, the colour part being 18–21 μ long. The persistent conidiophore is rigid, straight or curved to one side, and from 7–11 μ long. At the time of germination the lowest of the three coloured cells swells up, becomes globose, marked by a light ring round the middle, and then puts out a germ-tube from the sides (Fig. 121, *4*).

Age of the bushes, water-logging, undrained soil which is poor and worn out, favour this disease and make the host very susceptible to its attack. Clean pruning during the winter, together with the collection and burning of all diseased leaves, checks blight to a considerable extent. Blighted leaves should be carefully removed and burned throughout the spring so that the supply of infective material is reduced. Spraying with Bordeaux mixture once in winter and again in April or May has been suggested where pruning

and cleaning have not been done, but this does not usually give an adequate return for the money invested on materials and labour.

A large number of leaf-spots, blights, leaf-blotches, etc., due to species of *Alternaria*, *Cercospora*, *Cladosporium*, *Helminthosporium*, *Ascochyta*, *Colletotrichum*, *Phyllosticta*, *Septoria*, etc., occur on several crop plants, but in the majority of cases those diseases have not been carefully investigated in India, for the damage they have done and the losses they have caused, have not been appreciable. Unfavourable soil and environmental conditions usually favour these diseases, but where good cultivation is practised they can be checked to a considerable extent.

OCFEMIA, G. C., "The *Helminthosporium* disease of rice occurring in the southern United States and in the Philippines," *Amer. J. Bot.*, **11**, 385–408 (1924).

PADWICK, G. W., MITRA, M., and MEHTA, P. R., "The genus *Fusarium*. IV: Infection and cross-infection tests with isolates from cotton (*Gossypium* spp.), pigeon pea (*Cajanus cajan*), and sann-hemp (*Crotalaria juncea*)," *Indian J. Agric. Sci.*, **10**, 707–715 (1940).

RANDS, R. D., "Early blight of potato and related plants," *Res. Bul. Wisconsin Agric. Exp. Sta.*, 42 (1917).

RAYCHAUDHURI, S. P., "A disease of pigeon pea (*Cajanus cajan* (L.) Mills) caused by *Diplodia cajani* sp. nov.," *Indian J. Agric. Sci.*, **12**, 837–847 (1942).

VARADARAJAN, B. S., and PATEL, J. S., "Stem-rot disease of jute," *Indian J. Agric. Sci.*, **13**, 148–156 (1943).

SUNDARARAMAN, S., "*Helminthosporium* disease of rice," *Bull. Pusa Agric. Res. Inst.*, 128 (1922).

WOODROOF, N. C., "Two leaf-spots of the pea-nut (*Arachis hypogea* L.)," *Phytopath.*, **23**, 627–640 (1933).

CHAPTER X

BACTERIAL DISEASES OF PLANTS

THE announcement that bacteria cause disease in plants was first made in 1878 by T. J. Burrill of Illinois, who showed that fire-blight of pears and apples is due to a bacterium which he named *Micrococcus amylovorous*. A large number of plant diseases have since then been proved to be due to the activity of pathogenic bacteria, of which the most important in India are the 'ring disease of potatoes', 'canker of citrus trees' and 'yellow rot of wheat ears'.

Bacteria are plants without chlorophyll, with a saprophytic or parasitic mode of life, and, like fungi, are unable to synthesize their food requirements from inorganic substances in the presence of sunlight. Their structure is very simple, there being no distinguishable morphological feature other than shape (Fig. 122), of which there are four kinds: straight rods or bacillus, curved rod or spirillum, sphere or coccus, and filaments. They are the smallest plants, being 0·5–5 μ in diameter and up to 10 μ in length, and an average bacterial cell has a volume of one cubic micron. It is stated that in one cubic centimetre of water there can be about one trillion bacteria of average size.

A bacterial cell has a wall made of chitin, which is a nitrogenous substance closely related to carbohydrate. The cell-wall is thin and consists of a single layer. Some bacterial cells envelop themselves with layers of gelatinous material, or with membranes, known as capsules or sheaths. The protoplasm is not clearly differentiated into nucleus and cytoplasm, but the nuclear material, the chromatin, is scattered throughout the protoplasm. Inclusions of many kinds are found within bacterial cells, such as granules of food, sulphur, etc. A few species of cocci, many species of bacilli, and practically all species of spirilla possess organs of locomotion known as **flagella**. The lashing movements of the flagella give these organisms the power of locomotion. Bacteria without flagella are known as **atrichous**, and those with a single polar flagellum as **monotrichous**. If there is a tuft of polar flagella, they are known as **lophotrichous**, and if flagella are distributed over the entire surface, as **peritrichous**.

With the exception of certain kinds of bacteria, spore-formation is absent in these micro-organisms. In the species that produce spores only a single spore is produced endogenously within a cell, and the spores are known as **endospores.** None of the bacteria that cause disease in plants are spore-formers.

The principal method of multiplication of bacteria is by simple fission. A rod elongates to about double its original length and splits in the middle to form two individuals. Spherical cells frequently

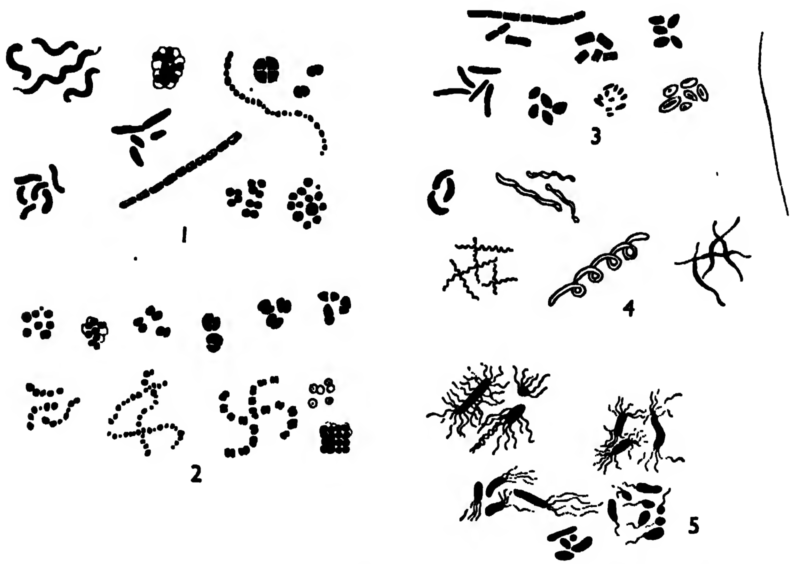


Fig. 122.—Bacteria: *1* types of bacteria, cocci, bacilli and spirilla; *2* various groups of cocci; *3* types of bacilli; *4* types of spirilla; *5* arrangement of flagella on bacteria (after Buchanan).

elongate before they divide. Bacteria multiply with considerable rapidity, certain forms being able to divide, if conditions of food and environment are optimum, once in every twenty minutes. A single bacterial cell, if the process continues, will form in two days 2^{96} of bacteria, a number with twenty-eight figures. But as optimum conditions for growth cannot long continue, obviously such bacterial masses are never found in nature.

Because of their very simple morphology, bacteria cannot be divided into orders, families, genera and species on the basis of their structural characteristics alone; biochemical, physiological and cultural characters have to be taken into account in their differentia-

tion. The class is divided into six orders, but plant-pathogenic forms occur only in the orders Eubacteriales and Actinomycetales. There has been a good deal of change and also confusion as regards plant-pathogenic bacteria. Erwin F. Smith, who did pioneer work in this field, accepted at first a system of classification proposed by Migula. This was based on the number and arrangement of flagella: *Bacterium* for non-motile rods, *Pseudomonas* for polar flagellate organisms, and *Bacillus* for rods with peritrichous flagella. In 1905 Smith introduced certain changes, proposing the name *Aplanobacter* for non-motile rods, *Bacterium* for polar flagellate organisms, and *Bacillus* for peritrichous rods. In 1923 Bergey introduced in his *Manual of Determinative Bacteriology* a new system for plant bacterial pathogens, placing peritrichous rods in the genus *Erwinia* and non-motile polar flagellate rods in *Phytomonas*. The system is rather arbitrary, and is not followed by all plant pathologists.

Bacteria, like fungi, can be stained. One of the principal stains used in bacteriology is the Gram's stain, which consists essentially in staining bacteria with one of the aniline dyes, usually gentian violet, adding a solution of iodine as a mordant, then decolorizing with alcohol. Some bacteria take this stain and others do not. Bacteria may be divided into two groups: those that are Gram-positive—that is, which retain the colour—and those that are Gram-negative—that is, which do not retain the colour.

Bacteria cause three types of diseases in plants: (1) vascular diseases or tracheo-bacterioses, (2) parenchyma diseases and (3) hyperplastic diseases. In the first type the pathogens are very abundant in the lumen of the xylem vessels in the early stages of the disease. This clogging interferes with the supply of water to the foliage, and the plants wilt in consequence. Bacterial wilt of tobacco due to *Phytomonas solanacearum* is an example of such a disease. In the parenchyma type of diseases the bacterium invades the soft and succulent tissues, causing necrosis without hyperplasia, resulting in rotting, as in soft-rot of carrots due to *Erwinia carotovora*, or spotting of leaves, as in angular leaf-spot of cotton due to *Phytomonas malvacearum*. The hyperplastic type of diseases is characterized by the formation of tubercles, tumours or galls, as in crown gall of fruit-trees due to *Phytomonas tumefaciens*.

Bacteria enter the host through wounds, stomata, water-pores and lenticels. Most of them enter through wounds. In pear blight it has been demonstrated that entry may take place through

nectaries. Direct entry by the penetration of the cell-wall occurs only in legume-nodule-producing bacteria. Bacteria are as a rule intercellular within the tissues of the host except in the case of nodule-producing forms on legumes, where they are intracellular. These diseases are disseminated by seed, by insects or other animal life, or by contaminated fertilizer like compost.

Bacteria act on the host by the production of enzymes that convert starches into sugars or digest the middle lamella, causing a separation of cells of the host tissue, by the formation of injurious toxins or by the production of substances which stimulate cells to abnormal activity.

In finding out control measures, it is essential to know the biology of both the host and the bacterium. In many instances where bacteria hibernate on or in plant-organs like seeds, tubers, roots and stems, disinfection by heat or chemical is resorted to. Similar methods are used in sterilizing soils. Selection of disease-free organs or plants is also useful. Spraying plants with germicidal (bactericidal) substances is effective in some cases. Crop rotation, proper timing of planting so as to avoid environmental factors that are favourable to the pathogens, and field sanitation—that is, destruction of diseased plant debris—are some of the methods employed with success. Eradication of diseased plants is a practice widely followed. In diseases which are disseminated primarily by insects, efforts should be directed towards the destruction of the insect itself. Since many bacteria enter through wounds, it is imperative to control all the agencies that break the protective surfaces of plants. Development by selection and hybridization of resistant varieties of plants promises to become one of the most important and economical control measures.

Ring Disease of Potatoes (*Solanum tuberosum* L.)

The ring or 'bangdi' disease of potatoes due to *Phytomonas solanacearum* (Smith) S.A.B. has been reported from most of the important potato-growing areas in India. The extent of its ravages is very great, and sometimes fields where the disease occurs have to be left fallow or sown with some cereal crop, as the cultivation of potatoes in such areas becomes extremely unprofitable.

The disease becomes manifest when plants suddenly wilt. One or two leaves may first show the symptom, but very soon the whole plant wilts and dries. If the tubers of an affected plant are

cut into two, they will almost certainly show a brown ring a short distance from the edge. This ring will be found to begin at the point where the tuber is attached to the underground stalk which bears it, and to spread from that point around to the other end of the tuber. In its initial stages, therefore, the ring is not complete, there being only a brownish streak at the point of contact. If a diseased tuber is cut and slightly squeezed, a series of small, creamy-white, slimy drops exude along the course of the brown ring, which consist of millions of bacteria, shaped like small short rods. If sections of the tuber at this region are examined, it will be found that these rods are confined chiefly to the vessels of the tuber. As the disease progresses, infection spreads to the whole tuber, which is turned into a rotten mass.

Stems, roots and tuber-stalks are invaded by the bacterium, which confines itself as a rule to the vascular elements, plugging them more or less completely, thus causing wilt.

The parasite is a small, rod-shaped organism, $1-1{\cdot}5\ \mu$ long and $0{\cdot}5\ \mu$ broad. It is motile by means of one polar flagellum and is without spores or capsules. It is Gram-positive and aerobic.

Ring disease is both a tuber-borne and soil-borne disease. Tubers harvested from fields where disease is present invariably carry infection. Badly affected tubers may not sprout, and though they germinate when infection is slight, the bacterium invades the vessels, and sooner or later the plants wilt. Soil-borne infection is also common, but infection through the agency of insects does not take place in India.

Phytomonas solanacearum has a wide host range, and many solanaceous plants, including tomatoes, brinjals and tobacco, are attacked by it. Several species of Musaceae, Commelinaceae, Leguminosae, Malvaceae, Acanthaceae, etc., are also attacked. So far, the bacterium has not been found to attack graminaceous hosts.

From what has been said above, it will be manifest that only those potato tubers should be used as seed which have been grown on a plot quite free from disease. Tubers from plots where the disease has occurred must be discarded, for they may carry infection even though they may not show the diseased ring. Fields where it has been prevalent should be left fallow for one or two years, and a cereal crop grown on it for a time before sowing a solanaceous crop. Spraying and dusting are, however, of no use.

Citrus Canker (*Citrus aurantifolia* Swing.)

Citrus canker due to *Phytomonas citri* (Hasse) S.A.B. is a wide-spread disease throughout the citrus-growing countries of the eastern hemisphere and occurs in a particularly serious manner in India, China, Java and Japan. It is stated to have originated some-

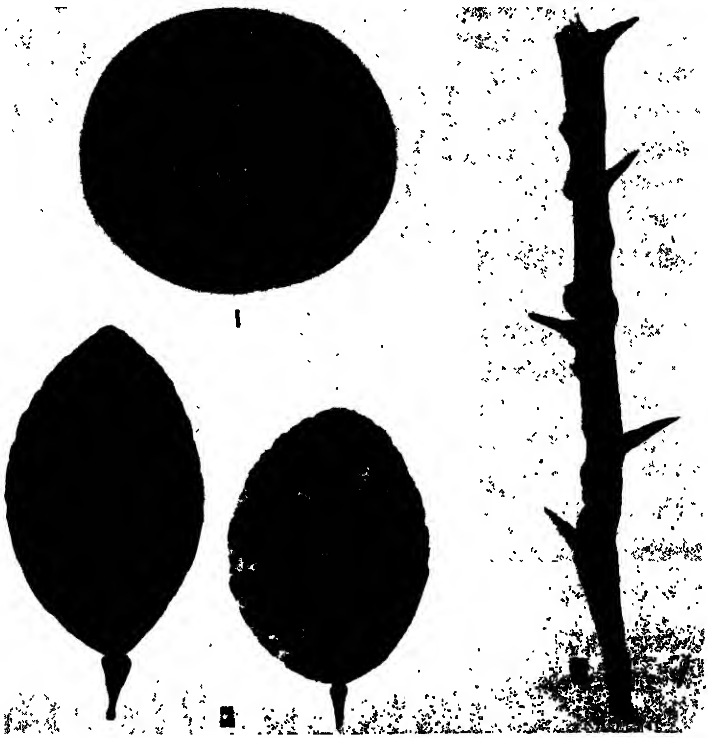


FIG. 123.—Citrus canker: *1* lesions on fruit; *2* lesions on leaves; *3* lesions on twigs.

where in south-eastern Asia, and on specimens of citrus plants collected at Dehra Dun between 1827 and 1831 and deposited at Kew Herbarium, cankers have invariably been found. The disease has not been found in Cuba, Puerto Rico, California and the Mediterranean regions, but it appears to have been recently observed in Cyprus and Palestine.

Canker may affect any part of the tree above the ground, although the leaves, twigs, young branches and fruits are the most susceptible

parts (Fig. 123). On the leaves, cankers first appear as small, watery, translucent spots, usually of a darker green colour than the surrounding tissue and with a raised convex surface. As a rule the spots first become evident on the lower surface, and as the disease advances, the surfaces of the spots become white or greyish and finally rupture, exposing a light brown, spongy central mass developed in a crater-like formation. These spots usually become surrounded by a halo which persists in very old lesions. Old lesions become corky and brown, and may sometimes appear pinkish. Lesions on the twigs are common on the more susceptible kinds of citrus, and on young twigs they are like those on the leaves and fruit, but on older twigs they are more or less irregular in shape, especially in the case of the old spots. The spots show the same spongy tissue as those found on the leaves, but acquire a cankerous appearance, and the surface membrane completely disappears. The canker lesions on the fruit have much the same appearance as on the leaves, except that the yellow halo is usually absent and the crater-like appearance is more noticeable. The spongy, rough eruptions may be scattered over the surface, or several may coalesce forming an irregular, scurfy, scabby mass.

Phytomonas citri is a short, rod-shaped organism, motile by means of a single polar flagellum. It is 1·5–3 μ long and 0·5–1·5 μ broad, enclosed in a capsule and strictly aerobic.

Citrus canker is favoured by mild temperature and wet weather. Temperatures between 20° and 35° C. appear to be most suitable, and in areas where the rainfall is well distributed, citrus canker thrives during the period when the temperature is between these limits. The disease is disseminated by wind and driving rains and by insects, especially leaf-miners. The chief agent of dissemination is, however, man who transports the disease on bud-wood or nursery trees.

Prompt and complete destruction of all canker-infected trees is the only safe and practical method that has been found for checking the disease. This can be done to best advantage by burning diseased parts. In India, where the disease has established itself primarily in most of the orchards, such destruction of trees is not possible, but pruning of infected twigs and foliage during the dry season to eliminate the sources of infection has been found to be a good practice. Spray applications with Bordeaux and lime sulphur materially lessen the disease. Such spraying should be directed primarily for the

FIG. 124.—Tondu disease of wheat; distortions of various kinds produced by the bacterium.

protection of the fruit, and to be most effective it should be done during the first three months after they are formed.

Not all species of citrus are equally susceptible to canker. *Citrus sinensis* Osbeck, *Citrus poonensis* Tanaka, *Citrus grandis* Osbeck are usually not attacked, whereas *Citrus jambhiri* Tanaka, *Citrus aurantium* L. and *Citrus aurantifolia* Swing., are among the most susceptible varieties. Improvement of citrus varieties by hybridization has not yet been taken up in India on a large scale, and hybrids with the required qualities and resistance to canker are not yet available.

Yellowing Rot of Wheat Ears (*Triticum vulgare* Host)

A disease of wheat characterized by the curling of the stalks and the inflorescence, and transformation of the spikelets into a bright-yellow, slimy mass due to a bacterium, *Phytomonas tritici* Hutchinson, is very common in some parts of the Punjab. The precise loss from this cause has not yet been ascertained, but as the affected ears fail to yield any grain, its appearance even in a mild form is bound to occasion a good deal of loss.

Diseased plants first show a wrinkling of the lower and twisting of the central leaves, accompanied by the exudation of a bright-yellow slime or gum over the affected parts (Fig. 124). This gum forms sticky layers between the glumes and between the stem and the sheath, and interferes with the growth of the plant, so that the stem becomes distorted. Abnormally small and slender heads may be formed, but the flowers become distorted also and do not develop further. If the atmosphere is humid, the slimy yellow mass can be seen trickling down, but when it is dry it becomes sticky and after a time turns hard and dry.

Phytomonas tritici is a motile rod with one polar flagellum, 2–3 μ long and 1 μ broad. It grows best at a temperature of 20–22·5° C., and its thermal death-point is at about 50° C.

The exact mode of transmission of this disease is not yet clearly known, but there is ample evidence to show that eel-worms which cause the ear-cockle disease in wheat transmit the bacterium. Methods of controlling it have not yet been found, but it is suggested that if the fields are well drained and cultivated, there is little chance of the disease appearing in an epidemic form.

CHAPTER XI

VIRUS DISEASES

In addition to fungi and bacteria, a third group of infectious agents that cause disease in plants are the viruses. They attack several crops of economic importance, there being as many as twenty viruses on the potato plant alone. Some virus diseases cause heavy losses, others do little harm, and there are a few that add value to the plants they attack by inducing variegation, as in the ' breaking ' of tulips.

Viruses are invisible, and so small that they cannot be seen even with the highest magnification of the microscope using visible light. They are ordinarily recognizable only by their biological activity—that is to say, by the disease they cause. At one time an element of mystery surrounded them, and they were variously regarded as invisible forms of bacteria, as protozoa, as enzymes, as toxins or as unusual products of cellular metabolism. In 1935, however, Stanley, an American biochemist, isolated by chemical means from diseased tobacco leaves a material which appeared to be a protein of high molecular weight. This material possessed all the properties of tobacco mosaic virus, and there is a great deal of direct, indirect and circumstantial evidence to show that it is the virus itself. Since then, by using similar methods or by means of centrifugation, proteins of high molecular weight possessing the properties of the respective viruses have been isolated.

The purified viruses consist largely of nucleo-proteins, some of which can be crystallized. Examination of the common tobacco mosaic virus with the recently developed electron microscope has shown that it is rod-like in shape, about 280 μ milimicrons ($m\mu$) in length and 18 $m\mu$ in breadth. No other morphological features are known.

Viruses can ordinarily be recognized by the symptom picture they produce on the host, which may be due to a single virus or in different combinations with other viruses. The same virus can cause widely different symptoms in different species of host plants, and symptoms may vary in the same plant with its age and its nutrition. Symptoms as a basis for identifying specific viruses are

thus not reliable unless a range of hosts is used and the symptoms produced on them carefully noted.

The most common symptom is chlorosis, and so prominent is it that at one time virus diseases were known as **infectious chloroses.** In some types of chloroses light-green masses of tissue of varying sizes and shapes are irregularly distributed in, and more or less separated from, the normal green tissue. In other words, instead of being uniformly green, the leaves develop spots, patches, rings or other patterns of light-green colour (Figs. 125, 126). This is the **mosaic** type of virus diseases. In another type, known as the **yellows** type, the chlorosis is general throughout the leaves, there being no mottling. The third type of symptom is **necrosis**, which causes groups of cells in a diseased plant to collapse and die. Necrosis occurs both in stems and leaves, and viruses of the necrotic type are common in the potato plants. In some virus diseases there are over-growths such as galls (Fiji disease of sugar-cane) or enations (sannhemp mosaic). Stunting and dwarfing of plants, crinkling, puckering and reduction in size of leaves, and sterility are some of the other symptoms. In fruits virus diseases cause insipidity, as in peaches from trees affected by yellows. Cucumbers from mosaic-diseased plants lose their shape, become knotty and twisted, and are unevenly ripened.

FIG. 125.—Virus-affected potato plant.

Virus diseases rarely cause complete death of the plants, for diseased plants may live as long as healthy ones. Affected plants become, however, predisposed to diseases due to fungi or bacteria. Premature and rapid death is not unknown, for tomato plants attacked by spotted wilt or potato plants attacked by necrotic viruses succumb completely.

Within the tissues of the host, virus diseases cause certain pathological changes, the most characteristic being the appearance of **inclusion bodies**, of which there are two kinds. The first are amoeba-like, amorphous bodies which are vacuolate and bear a rather superficial resemblance to protozoans. The second are crystalline in character, fragile, and extremely variable in shape. Such inclusions, both amoeboid and crystalline, seem to be an absolute characteristic of plants attacked by virus diseases. At one time they were considered to be reaction products of host-cell cytoplasm, but detailed studies of their formation have shown that they are neither the cause nor simple host-reaction products. They are the visible result of a union between the virus and other specific constituents of host cells.

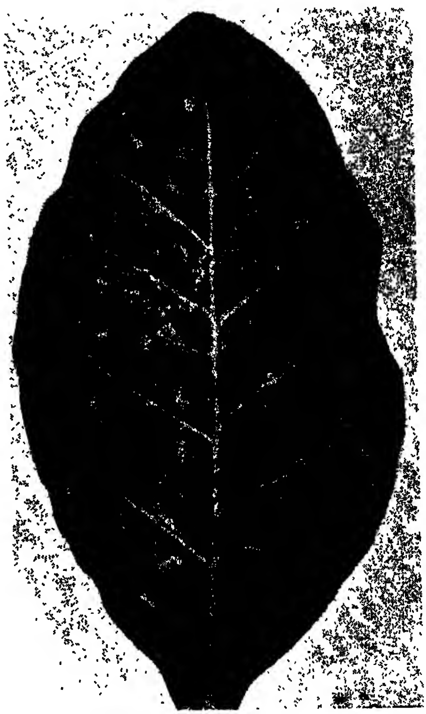


FIG. 126.—Tobacco leaf affected by virus.

Virus diseases are transmitted to healthy plants by grafting or other organic union between healthy and diseased plants. In fact, if a plant that shows all the symptoms of a virus disease is not graft-transmissible, and therefore not infectious, it may not be suffering from a virus disease. Seed transmission is relatively rare, there being only a few cases on record, of which mosaic diseases of leguminous plants and cucurbits are the most striking examples. Perpetuation of the disease from progeny to progeny in vegetatively grown crops like sugar-cane and potato is very common. As the viruses are usually spread throughout the host, they naturally occur in the dormant tissues, and the vegetative organs of reproduction, such as tubers, bulbs, rhizomes, etc., carry infection.

Another method of transmission is by inoculation or rubbing of the extracted sap of infected plants into healthy plants. Infection can be produced by this means in any part of the plant, the slightest abrasion, even broken or cut hairs, permitting entry. Uninjured plants, however, do not become infected.

The most general method of transmission is by means of sucking insects, of which aphids, jassids and white flies are the most important. In the field, dissemination is chiefly through their agency, and it is to a large extent true that if there were no sucking insects to serve as vectors, there would be no virus diseases. The spread of virus diseases in some cases is nothing more than a simple mechanical transfer. A single virus disease may be transmitted by several insect species, or a single insect may transmit several diseases. all cases where the insect makes a simple mechanical transfer it los its infectivity within a few hours.

Instances are known where an insect cannot infect a healthy plant soon after it has fed on a diseased plant. There ensues a delay in the development of infectivity which, with different viruses, varies from hours to days. In other words, there is an **incubation period** for the virus within the vector. What determines this specific relationship is unknown, but it appears to be obligate in character, the insect being apparently an alternate host in which the virus undergoes some change.

The precise relationship between the insect vector and the virus is not in some cases properly understood. Curly top of sugar-beet is transmitted by the leaf-hopper, *Eutettix tenellus*, but not by other sucking insects feeding on sugar-beet. Sugar-beet mosaic, on the other hand, is transmitted by the peach aphid, but not by the above leaf-hopper. Stunt of rice is spread by the leaf-hopper *Nephotettix apicalis*, but other leaf-hoppers that feed on rice plants are not able to transmit the disease. From plants that are simultaneously infected with mixtures of tobacco mosaic and cucumber mosaic viruses, tobacco mosaic alone is transmitted by needle prick, whereas aphids will transmit only cucumber mosaic virus.

A knowledge of the physical and chemical properties of the viruses in extracted sap is often very useful. The capacity of the sap containing the virus to withstand filtration, dilution, action of formaldehyde, and of enzymes like trypsin and pepsin, and the reaction of the viruses to ageing and to ultra-violet light at 0° C., and their thermal death-point, are precisely and carefully determined. But in

most cases the values obtained are not fixed values but are dependent on the virus content and purity of the suspensions. As purified preparations of several sap-transmissible viruses whose precise chemical composition is known, are now available, the physical and chemical properties of such preparations would give absolute and fixed values.

Attempts have from time to time been made to classify viruses. By studying the reaction produced on differential hosts, by assuming host-specificity, by determining their physical and chemical properties, viruses have been classified into families, genera and species. But there is as yet no agreement among virus pathologists about the precise diagnostic characters that should be used, and classification still offers a challenge to their ingenuity.

Virus diseases can be controlled in several ways. Ruthless eradication by rogueing, and burning of rogued plants, have given useful results. It is important to see that all underground parts are carefully removed. While seeds of crops other than those of legumes and cucurbits usually do not carry the virus, it is a good practice not to save seed from diseased plants. In potatoes 'tuber-indexing' has helped considerably in checking disease, as it aids in the elimination of infected tubers and in obtaining healthy stocks. For this purpose the tubers are carefully numbered with Indian ink, and a piece of each tuber, correspondingly numbered, is grown in pots in insect-proof houses and examined for symptoms of disease. After eliminating all those that show disease, the healthy stock is multiplied in isolated spots, first in the insect-proof houses and then at high altitudes where insect-borne infection is negligible.

Removal of susceptible weeds on which the virus over-winters or over-summers is also desirable. Since virus diseases are insect-borne, all measures against insect vectors constitute an important method of control. Spraying against insects, use of parasitic and predatory insects that prey on them, protection of the crop in the seed-bed with screens, form some of the means by which viruliferous insects can be checked.

The most promising method for effectively controlling virus diseases is by the development of varieties of plants that resist them. Sugar-cane mosaic has been controlled by the production of what are called P.O.J. varieties, one of the parents of which is the highly resistant Indian cane known as the 'uba' cane. A variety of tobacco known as 'ambalema' has been reported to be resistant to the

common tobacco mosaic virus. Curly top of sugar-beets has been controlled in the United States by the development of resistant varieties. Efforts to control potato virus diseases by similar varieties are also in progress, both in India and abroad.

In India many of the crop plants are attacked by virus diseases, and the damage they cause is sometimes considerable. None of the more important cereal crops is, however, attacked. There are two virus diseases on sugar-cane in India, mosaic and streak, but neither of them has so far been of much consequence. Tests conducted over a period of years have shown that the loss in yield due to sugar-cane mosaic is insignificant. Attacked plants recover during or after the monsoon, and natural spread in the field due to the insect vecto especially in northe India, is very rare.

FIG. 127.—Leaf-curl of tobacco, a virus disease.

A serious virus disease affects cardamoms (*Elettaria cardamomi*) in western India, especially in Kanara, Malabar and Anamalai Districts. Plants which ordinarily live, and yield, from fifteen or twenty years succumb to the disease within five years, causing enormous losses to the planters, as the crop is a lucrative one. Attacked plants are stunted and show mottling of the leaves. The vector of the disease has only recently been discovered to be the aphid, *Pentalonia nigronervosa*, which also transmits the bunchy-top disease of bananas.

A leaf-curl of tobacco (Fig. 127) is common in several parts of India, and preliminary work done some years ago has shown that five different kinds of symptoms can be detected. The leaves get so badly curled, twisted and distorted that they are rendered worthless for the market. Leaf-curl is transmitted by the whitefly, *Bemisia gossypiperda*. The same disease occurs on *Aegeratum conyzoides* and other weeds and is transmitted by the same vector. Strict rogueing in the seed-bed and later in the fields has helped in reducing

FIG. 128.—Papaya plant, affected by leaf-curl.

the intensity of the disease, and spraying with nicotine sulphate has shown much promise.

Mosaic disease of cucurbits occurs wherever cucurbits are grown in India; more than two viruses are present, but the extent of loss due to each has not yet been definitely ascertained. Distortion of the fruit, which is such a common symptom of this disease in the United States, has not been observed in India.

Ground-nut rosette was first reported from southern India in 1926, and is gradually increasing in importance there. Attacked plants are stunted, their leaves turn creamy-yellow and are reduced in size, and yields are very much diminished.

Five potato virus diseases have so far been definitely identified in India—namely, leaf-roll, virus *X*, *Y*, *A* and *D*—but others await precise determination. As a result of attack by these diseases, the cropping power is lost, the tubers when formed are usually reduced in size, and they lose their keeping qualities. Seed certification to ensure distribution of healthy stocks to the farmers has been introduced, and this should ensure relatively virus-free potato crops.

Virus diseases of beans, pigeon peas, sann hemp, cotton, bhindi (*Hibiscus esculenta*), brinjals, chillies, tomatoes and papayas (Fig. 128) have been observed, but only a few of them have so far been investigated. Measures to control them are therefore not precisely known.

CHAPTER XII

PLANT DISEASE CONTROL

METHODS of controlling some of the specific plant diseases have been briefly indicated in the preceding pages. Before discussing them more fully, the intricate relationship between the agents that cause disease and the host plants thus affected deserves close study. When a disease occurs in a severely epidemic form, the organism is said to cause an **epiphytotic**. The three conditions necessary for its development are: (i) abundance of the parasite, (ii) occurrence of a susceptible host and (iii) presence of conditions favourable for the development of both the host and the pathogen.

Plant-parasitic fungi have adapted themselves quite well to a pathogenic mode of life. Their abundance at a given time for producing epiphytotics is ensured by their capacity to produce, in the same species, a variety of spore-forms (pleomorphism), branched sporophores, chains of spores, and multi-celled and muriform spores, and by their capacity sometimes to bud. Their liberation is effected by devices for hygroscopic movements of the fructifications, by abjection and ejection of spores, and by increasing the duration of spore discharge so that an adequate supply of spores is available over a considerable period of time. Their dissemination is secured through the agency of wind, water, insects and seed, or plant parts functioning as seed, such as tubers, setts, corms, rhizomes, bulbs and nursery stock. Germination of spores, their entrance into the host tissue and their spread within, are governed by environmental factors, and when these are not favourable the chances of a disease becoming an epiphytotic are remote. A knowledge of the complete life-history of the causal organism and the several reproductive structures it produces to suit different conditions is thus highly essential.

A species of a fungus is a taxonomic concept, but to a plant pathologist a species stands for something more. As fungi respond differentially to environmental conditions, their plasticity has to be recognized, and a species therefore represents not only a totality of individuals with a morphological resemblance among themselves and their progeny, but possesses essentially similar physiological and parasitic qualities. The recognition of these facts has led to the

discovery of the phenomenon of **parasitic specialization**, an understanding of which is highly desirable.

Parasitic specialization presumes that there are, within well-defined morphological species of fungi, entities which are not easily distinguishable by morphological characters but which differ from each other in their physiological and parasitic characters. These entities, known as **physiological races**, are distinguished on the basis of their cultural characters, physico-chemical reactions and pathogenicity.

Many parasitic fungi can be grown on culture media, and it is possible to distinguish races in them by differences in their growth colour, consistency, topography of the surface and other characteristics. Such races are termed 'cultural races' to distinguish them from 'parasitic races', which are differentiated only by their capacity to infect certain species or varieties of plants and not others. There is no direct or satisfactory evidence, so far, to correlate cultural races with parasitic ones.

Parasitic races are actually classified into two categories: **varieties** and **races**. Parasitic varieties are distinguished to a small extent by their morphology, but chiefly by their capacity to infect certain species of one or more genera of a family but not species of other genera of the same family, which may, however, be attacked by another parasitic variety of the same fungus. A parasitic variety in turn comprises several physiological races which differ from each other by their ability to attack varieties within one or more species of a host genus. Thus the parasitic variety attacking wheat is *Puccinia graminis tritici*, and that attacking oats is *Puccinia graminis avenae*. Within the parasitic variety *Puccinia graminis tritici* there are about 180 races, which are distinguishable by their parasitic behaviour on twelve differential hosts selected for this purpose by Stakman and his colleagues. These are given below:

Triticum compactum
Little club

Triticum vulgare
Marquis
Reliance
Kota

Triticum dicoccum
Vernal
Khapli

Triticum durum
Arnautka
Mindum
Kubanka
Spelmar
Acme

Triticum monococcum
Einkorn

When the above species and varieties of wheat are infected by a collection of rust, the following symbols are used to indicate the type of infection which in due course appears on the seedlings:

(0) **Immune.** No uredia; hypersensitive flecks present, but sometimes there is absolutely no trace of mycelial invasion.

(1) **Very resistant.** Uredia minute, isolated; surrounded by sharp, continuous hypersensitive necrotic areas.

(2) **Moderately resistant.** Uredia isolated and small to medium size; hypersensitive areas present in the form of necrotic halos or circles; pustules usually green, but slightly chlorotic, islands.

(3) **Moderately susceptible.** Uredia medium size; coalescence frequent; development of rust somewhat subnormal; true hypersensitiveness absent; chlorotic areas may be present under favourable conditions.

(4) **Very susceptible.** Uredia large and generally confluent; true hypersensitiveness absent, but chlorosis may be present when cultural conditions are not favourable.

(X) **Heterogeneous.** Uredia variable, apparently including all types and degrees of infection, often on the same blade; no mechanical separation possible; on re-inoculation small uredia may produce large ones and *vice versa*.

While the above are types of infection, symbols have also been assigned by Stakman to indicate degrees of infection. These symbols are described below:

(=) **Trace.** Uredia very few, covering a limited surface; development of rust generally poor and decidedly subnormal.

(—) **Slight.** Rust development below normal but somewhat better than trace.

(±) **Moderate.** Variation in rust development from slight to considerable; when infection is uniform but medium in quantity, symbol is omitted.

(+) **Considerable.** Infection better than normal; uredia fairly numerous and scattered.

(++) **Abundant.** Luxuriant development of rust; uredia numerous, covering large areas of host.

(;) **Hypersensitive flecks.**

(.) **Necrotic lesions.**

For the determination of the race to which a rust collection belongs, seedlings of the differential hosts are raised in small pots, and when they are seven to eight days old, they are inoculated with the rust collection, taking all the required aseptic precautions. The inoculated plants are incubated for twenty-four hours in a moist chamber and later placed in the greenhouse inside a muslin cage to protect them from stray rust spores. When the pustules appear, the behaviour of the rust as to type and degree of infection is compared with the analytical key to the physiological races which Stakman publishes once in every five years. If the readings agree with those due to a particular race, the number of that race is assigned to the collection. Sometimes there may not be agreement, and the collection may be a mixture or a new race. Further inoculations are then necessary to settle the matter.

Physiological races are stable, and are not changed by environmental factors. They arise by mutation and hybridization; in *Puccinia graminis*, for example, such hybridization takes place in the protoaecium formed on the barberry.

Prevalence of a susceptible host is another condition for the occurrences of epiphytotics. The requisite host must not only be present, but it must also be susceptible and predisposed to attack. When a plant is rendered more susceptible to a parasite than plants of the same variety normally are, then it is said to be **predisposed.** Predisposing factors operate only on the plant, and render it more susceptible than it would otherwise be in the absence of these factors. Such factors are drought, winter-killing and alkali land. Environmental factors are not, strictly speaking, predisposing factors, as they affect both the host and the parasite.

But plants vary greatly in their liability to disease. In crop plants there are as a rule varieties which are specially predisposed to attack by a fungus, while other varieties of the crop are relatively free from attack. A variety of a crop that is a hundred per cent resistant is termed **immune**, but such immunity can only be relative and not absolute. Immunity from or resistance to a particular disease does not imply resistance to another disease. Even the resistance of one part of a plant may not be the same as that of another. Only natural immunity or resistance occurs in plants, acquired immunity or resistance having little significance, if any, in the plant kingdom. Then, again, immunity or resistance may be due to avoidance or endurance of disease, or to true resistance of disease.

Plants often avoid disease by maturing quite early. Varieties of wheat that mature earlier than others escape loose smut because the inoculum is not present to infect the ears at the time of their flowering. Early varieties of potatoes escape late blight, whereas the late crop is ruined, because the disease does not often begin to spread until the latter is ripening. Early maturing varieties of gram escape rust because the disease does not appear as a rule before the middle of February in northern India. Late-maturing varieties, however, become heavily infected.

Plants endure disease by being more vigorous—that is, because their tissues are able to react in such a manner that they can withstand attack. The more vigorous the plant is, the more rapid and complete the protective reaction. Sometimes, however, successful infection occurs only on healthy and vigorous plants. White rust of mustard does not develop in a severe form unless the host is in a flourishing state. The development of uredia of rusts does not take place in a host if its vitality is low, so that rapid spread of the disease is interfered with. The vigour of the rust in such cases is directly proportional to the vigour of the host.

Plants that are immune from or resistant to disease depend on morphological and physiological characters for immunity or resistance. The former may be affected by environmental changes, but physiological resistance is of a specific hereditary nature and is not easily influenced by environmental conditions.

Morphological resistance depends on the character of the epidermis and the cell-wall, both of which may offer resistance to penetration of the parasite into the host tissue. The size and number of stomata have a direct relation to the resistance which a variety of a crop offers to fungal invasion. In wheat-rust, infection of the leaves is conditioned by the number of stomata, by the size of their aperture, and by the movements of their guard cells. If within the stem tissues of the wheat plant there is an abundance of sclerenchyma as against collenchyma, the stems are rendered more resistant. In cotton plants the penetration of the mycelium into the vascular tissues is prevented by the formation of a corky endodermis round the stelar region.

Physiological resistance seems to depend on very complicated interactions between the protoplasm of the host cells and that of the parasite. Very little is as yet known concerning this type of resistance. Several theories have been advanced, but as yet none has

been definitely proved correct. Apparently there are substances in the host cells or in the plant juices which make it impossible for the parasite to grow normally. In the case of seedling blight of wheat and maize, susceptibility appears to be correlated with the ability to develop hexoses and polysaccharide building substances at various temperatures. Juices of onion varieties resisting attack by *Colletotrichum circinans* contain protocatechuic acid which is able to kill the germinating spores. In susceptible varieties this acid is absent.

Such resistance and susceptibility are therefore stable hereditary characters, and so dependent on genetic factors. In some cases they are controlled by a single genetic factor-pair, as, for example, in cabbage yellows due to *Fusarium conglutinans*, where resistance is governed by a single factor-pair. In most studies of the reaction of particular physiologic races to black rust of wheat, where the parents react reciprocally to the races, it was found possible to combine resistance to both forms in a single variety. Resistance in emmer and durum wheats has been transferred to vulgare wheats by crosses between varieties belonging to these two groups, only because a single genetic factor-pair was responsible for resistance. In other cases, however, resistance and susceptibility are dependent on multiple factors. In cotton more than two genetic factor-pairs appear to be concerned in deciding whether a variety is resistant or susceptible to wilt due to *Fusarium vasinfectum*. The same is true of linseed wilt due to *Fusarium lini*. When several genetic factors are involved, the calculation of the number of factors becomes the task of the geneticist, who determines them by the involved process of studying linkage relations with factors of known linkage groups.

The methods of investigation usually followed in finding immune or resistant varieties can be placed in three categories: (1) testing the domestic and foreign varieties; (2) selection; and (3) hybridization. Testing of established varieties occurring in a country is naturally the first step in the search for resistant varieties. Varieties of wheat resistant to loose smut have been obtained in this manner at New Delhi. This method is usually supplemented by the introduction of foreign varieties, if necessary. Gram blight due to *Mycosphaerella rabiei* has been successfully controlled in the Punjab by introducing foreign varieties and making selections to meet particular requirements. A large number of foreign wheats, potatoes and other crop plants are usually under test at different experimental stations in India to find varieties resistant to various diseases.

If the desired type of a crop is not found among established varieties or selections, then the next avenue of pursuit is hybridization. **Jayawant**, a wilt-resistant cotton in the Bombay Presidency, was obtained in this manner. It has the required agronomic and commercial characters of the susceptible parent, and the wilt resistance of the second parent. The same is true of **Verum**, another wilt-resistant cotton of the Central Provinces. Before making crosses it is necessary to obtain parents which exhibit certain desirable characters. Otherwise the effort may end in failure.

The last requisite essential for the occurrence of epiphytotics is the prevalence of environmental conditions favourable for the development of both the host and the parasite. The etiology of disease had until recently been considered too narrowly as concerning the immediate and apparent cause, viz., the parasitic agent. The antecedent factors that influence disease epidemics had been lost sight of. Environmental conditions not only influence the development and severity of plant diseases but also their distribution. It has been found that while wide extremes may be tolerated by crops, the parasite has a lesser range of adaptation to its environment. The prinicpal environmental conditions are those of weather and soil.

Numerous examples showing the relation of weather to disease development can be cited, for a great deal of research has been done. Taking Indian examples alone, Karnal bunt of wheat due to *Neovossia indica* occurs as an epiphytotic only when there is abundant rain, and air and soil temperatures are around 15–20° C., two to three weeks before blossoming time. The rain-water soaks the spores thoroughly, and the cool temperature promotes their germination. In the absence of both these conditions, the disease is rare. If there is abundant rain in January, and also in February, rust epidemics in wheat are very severe. This is true also of linseed rust. *Colocasia* blight due to *Phytophthora colocasiae* occurs only in the rainy season, especially when there is a continuous spell of moist and cloudy weather; plants recover as soon as dry conditions return. Downy mildew of maize is relatively rare in years when rains are below normal, but when there is excessive rain the disease appears in a severe form. Late blight of potatoes does not occur in the plains of India, where it is a winter crop and the conditions necessary for the growth of the fungus do not exist at the time. On the hills, on the contrary, where the crop is grown in the rainy season, late blight is

very severe. Sann-hemp wilt due to *Fusarium udum* var. *crotalariae* occurs in soils when their temperature is between 28° and 33° C., but pigeon-pea wilt due to *Fusarium udum* is common only when soil temperature is between 19° and 29° C. Stem-rot of patwa (*Hibiscus sabdariffa* var. *altissima*) due to *Sclerotinia sclerotiorum* appears in the crop only in the first or second week of January and never before, because the ascospores which alone can infect are not formed in summer or autumn, but only in winter.

Regarding soil type, it has been noted that in Gujerat root-rot of cotton does not occur in black cotton soils, where wilt alone occurs. Root-rot is common, however, in light soils. Even though both these soils are alkaline, they differ in their texture and other physical properties. In India cotton wilt occurs only in heavy black cotton soils that are alkaline, whereas in the United States it occurs in light sandy soils with an acidic reaction.

The influence of soil fertility on disease development is illustrated by the familiar example of wheat growing in soils heavily manured with nitrogenous manures. In such soils the severity of rust is enormous. If, however, the soil receives a balanced fertilizer with a slight excess of potash, the incidence of rust is comparatively light. Downy mildew develops in a severely epiphytotic form on jowar grown in soils that have been heavily manured, but the disease is absent or negligible if the crop is grown in plots that have not been manured or only slightly manured.

While immune or resistant varieties of crops offer an effective means of disease control, there are other efficient methods by which these hazards can be avoided. The selecting and breeding of resistant varieties are time-consuming processes, while these alternative methods can be more quickly applied. The first among these is **quarantines**.

With the extension of transport facilities at the present time, it is becoming increasingly difficult to control the movement of diseased plant material or other agencies that transmit disease. The risk of introducing new and unknown parasites into a country is therefore considerable. Such new parasites upset the equilibrium which existing pathogens and their hosts have established between themselves through several centuries by exposing the latter to attacks by the former and thus eliminating the more susceptible individuals. In most agriculturally advanced countries, therefore, plant quarantine legislation has been placed on the statute-book to restrict the move-

ment of diseased plant material or of fungi, bacteria or viruses, that cause disease in plants. In India a ' Destructive Insects and Pests Act ' was passed by the legislature in 1914, and it has been amended from time to time. Quarantines have been imposed by enforcing embargoes, by inspection at the point of origin and/or destination, and by disinfecting the material. Potato tubers are not allowed to enter India unless they are accompanied by a certificate from an Officer authorized by the Ministry of Agriculture of the importing country, stating not only that the tubers are free from wart due to *Synchytrium endobioticum*, but that there was no wart disease within a radius of five miles of the plot where they originated. By this means this dangerous disease has been successfully kept out of India. Cultures of fungi and bacteria are not permitted to be brought into India unless their entry is authorized by the Mycologist of the Government of India, who, before issuing a permit, satisfies himself that the particular organism is not a parasite in its country of origin or likely to be a parasite in India. Strict enforcement of quarantines means much cost, condemnation and abandonment of crops, loss of markets, and losses from possible retaliatory measures, for quarantines have often been used as tariff walls to exclude plants or plant products to the detriment of the consumer. Some pathologists think that the net gains due to the imposition of quarantines are negligible, and they therefore oppose the practice.

Another effective method of avoiding disease is by **eradication.** This can be done in several ways, such as: (1) eliminating the alternate hosts, (2) removal of infected parts, (3) eradication of wild hosts and weeds, and (4) rogueing. The intensity of black stem-rust has been greatly reduced in the United States by the systematic removal of barberry, the alternate host of the rust. Sugar-cane smut is best controlled by rogueing, for no other direct method is so far known.

Disease-free crops can be successfully raised by growing them in soil that is not infested by pathogenic fungi or in soil that has been disinfected by dry heat or steam, or by the use of chemicals. The use of dry heat or steam is very expensive, and under Indian conditions it will never become popular. Formalin diluted 1 : 20 to 1 : 50 is applied to the soil at the rate of two quarts per square foot in betel vine ' barojas ' to reduce losses due to wilt caused by *Sclerotium rolfsii*, and with considerable success. Bordeaux mixture of 4–4–50 strength is applied to such soils to prevent foot-rot of the

same crop due to *Phytophthora parasitica*. It must be noted that these methods are profitable only if the crops are remunerative enough to meet the extra cost.

The use of clean seed to avoid disease is, of course, a good practice. Such seed can be obtained from areas where a particular disease is unknown. It can be raised even in areas where the disease occurs, according to the nature of the disease. The crop in such cases must be carefully observed to ensure that, if diseased plants appear, they are immediately rogued. Wheat seed free from loose smut infection is obtained in this manner in small plots. Seed for such a plot is treated, and when the plants are coming into ear the plot is closely watched and all smutted plants that may appear are carefully rogued before they are able to do any harm. To obtain virus-free seed-potatoes 'tuber-indexing' is practised on a large scale in the United States and Canada. The method is described on p. 219. In some countries the use of certified seed is obligatory, and this has helped in considerably reducing losses from seed-borne diseases. Certified seed is seed from crops raised in fields that have been certified by plant-protection inspectors to be free from disease.

Disinfection of seed by the use of chemicals or heat is a well-known method of avoiding disease. Chemicals can be applied by the dip method, by spraying the seed with disinfectant, or by using the chemicals in a dust form. In disinfecting by the dip method, the seed is loosely packed in gunny-bags and the bags are dipped in a solution of the chemical of prescribed strength for a prescribed length of time. The seed is afterwards dried. The spray treatment is principally adopted against smuts of oats, using formalin. Concentrated formalin is placed in a pressure sprayer along with an equal quantity of water. The seed is spread on the ground in a thin layer, and the chemical is sprayed on it under pressure. The seed is stirred and afterwards placed in a heap and covered with clean gunny-bags to prevent the escape of the formaldehyde gas which kills the spores. The operation is done in the evening, and by the next morning the seed is ready for sowing.

By far the simplest method of seed treatment is to use chemicals in dust form. The dust must be of extreme fineness—that is, capable of passing through a sieve with 300 meshes per linear inch—otherwise it will hardly be effective. The seed is placed in a home-made seed-treating drum (Fig. 129) until it is half full, and the

requisite quantity of the dust is added. The drum is rotated for five to ten minutes, and the seed is by that time ready for sowing.

Disinfectant dusts are made from: (1) organic mercury compounds, (2) copper compounds, (3) non-metallic organic compounds, and (4) sulphur. The principal organic mercury compounds used are ethyl mercury phosphate, ethyl mercury chloride and chlorphenol mercury, sold under the trade names of Ceresan, Semesan and Agrosan. The effective chemical in these proprietary products is not more than 5 per cent, the rest being inert material. The usual

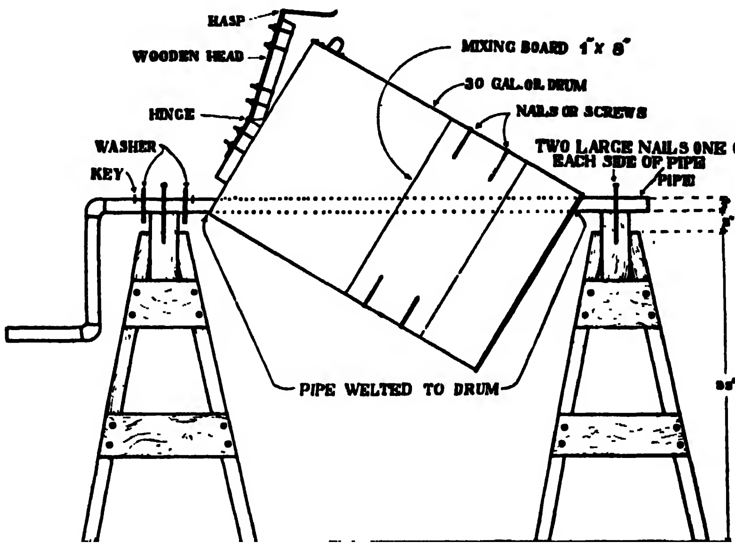


FIG. 129.—Seed-treating drum.

dose is one part of the disinfectant to 300 to 500 parts of seed. This of course varies somewhat with the crop and the disease. Copper is used in the form of copper carbonate dust, or red, yellow, brown or black oxides of copper. Among non-metallic dusts are Spergon (tetrachloro-*p*-benzoquinone), Thiosan and Arasan (tetramethylthiuram disulphide). In all these cases care must be taken to see that seed coverage is thorough and that treated seed does not clog the seed-drills. Seeds of some crops are sensitive to copper oxides, and should therefore be treated with other dusts when necessary. Seeds of cruciferous plants are as a rule treated with Ceresan or Spergon and not with dusts containing copper.

In dealing with seed which carries infection internally, the hot-water treatment is most effective. The method of treating wheat against loose smut which is internally seed-borne is described on p. 138.

The use of sprays and dusts to protect plants against disease is a standard practice. The cost of spraying must, however, be materially less than the loss which a disease may occasion, and the procedure must also be simple. Spraying is a prophylactic rather than a curative measure, and metallic ion in the spray inhibits germination of the fungus spores or kills the germ-tubes; once infection has occurred, sprays are of little use. Among annual crops, potatoes chillies, peas and ground-nuts are benefited by spray programmes because the margin of profit is appreciable and the extra yield that results more than offsets spraying costs. In the case of cereal crops sprays are too expensive, but for perennial crops like apples, peaches, mangoes and citrus fruit, spraying and dusting is quite essential.

Among the principal sprays are Bordeaux mixture, Burgundy mixture, lime-sulphur, Dithane and Fermate. Methods of preparing them are given below.

Bordeaux mixture, developed by Millardet in 1882, is very efficient against endoparasites like the downy mildew of the grape. The following substances are used in its preparation:

(1) Hydrated form of copper sulphate, $CuSO_4 \cdot 5H_2O$, purity 98 per cent.

(2) Quicklime or slaked lime.

Lime should be free from earth or sand and have a high calcium and low magnesium content. It is used as quicklime or slaked lime. The former is prepared by burning limestone. Slaked lime is prepared by slaking quicklime with water. Commercially available hydrated lime is the best source, provided it is stored in sealed containers; if exposed to air, it slowly reverts to carbonate form, which is worthless for the preparation of Bordeaux mixture. There are several formulae for preparing Bordeaux mixture, the chief being the following:

BORDEAUX MIXTURE 4–4–50

Copper sulphate	4 lb.
Quicklime	4 lb.
Water	50 gallons

BORDEAUX MIXTURE 5-5-50 (one per cent)

Copper sulphate	5 lb.
Quicklime	5 lb.
Water	50 gallons

Preparation of the spray, using the second formula, is as follows:

(1) Dissolve 5 lb. of bluestone (copper sulphate) in 25 gallons of water in a wooden cask.

(2) Slake 5 lb. of quicklime with a small quantity of water and add the paste formed to another 25 gallons of water in a second wooden cask.

(3) Stir the solutions, and then pour them simultaneously through a strainer into a third vessel or the spraying tank.

(4) Test the mixture for acidity.

It sometimes happens that the lime used is of poor quality, and the finished spray may contain a certain amount of free copper sulphate. This must be corrected to avoid spray injury, for free copper has a deleterious effect on foliage. A strip of blue litmus-paper is dipped into the layer of clear liquid on top of the spray; if the colour changes to red, then an excess of copper sulphate is present, and more lime must be added. A rough test is given by allowing a clean knife-blade or bright iron nail to remain in the mixture for a few minutes. If on removal this shows a brown coating of copper, more lime is required.

Bluestone is often difficult to dissolve. It is therefore best to tie it in a piece of gunny sacking and leave it suspended in the top of half the water for a few hours or overnight. By the next morning all the material will have dissolved. Copper sulphate is sold in a finely powdered and granulated form, commercially known as 'copper sulphate snow'. It dissolves quickly and can be added direct to water in the spray tank, solution being obtained by vigorous agitation. The required amount of hydrated lime is then washed into the tank through a sieve and the mixture is ready.

Bordeaux mixture must be used as soon as possible after preparation, as it loses its gelatinous nature if allowed to stand for some hours, and settles out. It should not be applied during rain, or on an exceptionally hot day or when plants are wilted or weakened by drought.

If good lime is not available, washing-soda can be used in preparing the mixture, which is then termed Burgundy mixture. It is

made exactly like Bordeaux mixture, but soda is used instead of lime. A formula is given below:

TWO PER CENT BURGUNDY MIXTURE

Copper sulphate	10 lb.
Washing-soda	12·5 lb.
Water	50 gallons

In applying sprays care must be taken to use the precise strength. The actual strength of the mixture most suitable for use depends on the type and age of the foliage that is to be sprayed, and no general prescription can be recommended. The younger the foliage, the weaker must the Bordeaux mixture be. The more alkaline the mixture, the less liable it is to cause foliage injury, but too much lime may injure fruit and other plant parts. Thorough coverage is achieved by adding a spreader to the spray fluid to increase the area of spread of the drops. The performance of the spray is thus improved. Emulsified cotton-seed oil or linseed oil have been used for this purpose. Stickers are added to improve the tenacity of the spray, so that it is not easily washed off. Among the principal stickers is casein.

Another spray fluid that is generally used for spraying, especially on fruit-trees, is lime-sulphur, which appears to be best against ectoparasites like powdery mildews. It can be bought ready-made in concentrated form and diluted as directed. Nowadays very few orchard growers and farmers prepare it themselves, both because of the trouble involved and because the ready-made concentrated preparations mentioned above are easily available. Moreover, the newer fungicides that need only dilution on the farm are not only readily available, but are several times more effective, so that lime-sulphur has lost most of its importance as a spray liquid.

Of the newer fungicides, organic sulphur compounds in the form of thiocarbamates have come into prominence and have been found to be very effective in controlling disease. Chief among them are Dithane (disodium ethylene bisdithiocarbamate) and Fermate (ferric dimethyldithiocarbamate). Dithane is water-soluble, and very tenacious on drying. If small quantities of zinc sulphate and lime are added to it, its fungicidal value increases tremendously. The spray, which is sold in a concentrated form, is finding favour because in order to prepare it one has only to add the required quantity of water. Fermate is sold as a black powder, and can be applied as a

dust or as a spray. It does not cause foliage injury or interfere with photosynthesis, as lime-sulphur does.

The choice of sprayers for applying the fungicides requires much care and thought. They range from hand atomizers through various types of hand and knapsack sprayers, pressure sprayers, barrel-pump sprayers, to large power sprayers, and the recently developed speed sprayers. The time, rate and pressure of spraying and the quantity of spray that should be applied to obtain proper coverage, are all

FIG. 130.—Spraying tobacco plants at Pusa.

matters for investigation for each different crop in each different location.

The application of fungicides in the form of dusts has superseded spraying, for dusting has certain advantages. The factor of abundant water supply vanishes, and the difficulties of preparation are reduced. Dusting apparatus is less cumbersome. Dusts must be of extreme fineness. Sulphur dust, which is widely used, is less effective as a fungicide than lime-sulphur, but it has found favour on account of its ease of application. For the application of dusts, 'dust blowers' or 'dust guns' are available, and with a little practice, can be operated without much difficulty.

INDEX